THE MAMMALS OF PARACOU, FRENCH GUIANA: A NEOTROPICAL LOWLAND RAINFOREST FAUNA PART 2. NONVOLANT SPECIES

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ABSTRACT

This report describes the results of nonvolant mammal inventory fieldwork at Paracou, a lowland rainforest locality in northern French Guiana, and concludes the faunal analysis introduced by our previous monograph on the bats of Paracou (Simmons and Voss, 1998). Working within a 3–km radius over the course of 202 sampling dates from 1991 to 1994, we recorded a total of 64 nonvolant species by conventional trapping, arboreal platform trapping, pitfall trapping, diurnal and nocturnal hunting, and interviews with local residents. Included in this total species count are 12 marsupials, 9 xenarthrans, 6 primates, 10 carnivores, 5 ungulates, and 22 rodents.

Systematic research with nonvolant mammal specimens collected as voucher material resulted in the discovery of new taxa, documented range extensions of previously described species, and helped resolve many longstanding taxonomic problems: (1) *Gracilinanus emiliae* (Thomas), herein reported for the first time from French Guiana, is redescribed and its known geographic distribution documented; based on examination of type material and original descriptions, *G. longicaudus* Hershkovitz is considered a junior synonym of *G. emiliae,* but *Marmosa agricolai* Moojen is not. (2) A new genus is proposed for *Gracilinanus kalinowskii* Hershkovitz, a taxon previously known only from eastern Peru, in recognition of its trenchant morphological differences from all other known didelphimorph marsupials. (3) *Marmosops parvidens* (Tate) and *M. pinheiroi* (Pine), the latter originally described as a subspecies of the former, are distinct species that occur sympatrically at Paracou; based on examination of type material, other taxa hitherto synonymized with *M. parvidens* are also judged to be valid species, including *M. juninensis* (Tate) and *M. bishopi* (Pine). (4) *Monodelphis brevicaudata* (Erxleben), *M. glirina* (Wagner), and *M. palliolata* (Osgood) are all distinct species diagnosable by unique combinations of morphological traits; based on examined specimens, *M. brevicaudata* (with type locality emended herein as Kartabo, Guyana) appears to be endemic to the Guiana subregion of Amazonia and to include both bicolored and tricolored phenotypes; a neotype from Cayenne, French Guiana, is designated to fix the application of *Viverra touan* Shaw as the oldest available name for the tricolored form. (5) *Saguinus midas* (Linnaeus) and *S. niger* (E. Geoffroy), currently treated as synonyms or conspecific races, are unambiguously diagnosable species that do not appear to be sister taxa; a neotype is designated to conserve current usage of *niger* E. Geoffroy for the black-handed tamarin of southeastern Amazonia. (6) Two new small species of *Neacomys* are described from material collected at Paracou; their diagnostic attributes are documented by detailed comparisons with other like-sized congeners from northern South America. (7) *Nectomys melanius* Thomas is recognized as a species distinct from *N. squamipes* (Brants) and *N. palmipes* J. A. Allen and Chapman; however, *N. parvipes* Petter is not a valid taxon and is herein synonymized with *N. melanius.* (8) The diagnostic characters of *Neusticomys oyapocki* (Petter and Dubost), a species previously known only from the holotype, are reevaluated and illustrated from freshly collected material. (9) *Oecomys auyantepui* Tate and *O. paricola* (Thomas), previously treated as synonyms, are valid species distinguished by consistent cranial differences and occupy allopatric ranges north and south of the Amazon, respectively. (10) A critical examination of small *Oecomys* specimens from Paracou and other Guianan localities supports the conclusions of other investigators that *O. rutilus* Anthony and *O. bicolor* (Tomes) are unambiguously diagnosable species. (11) *Oligoryzomys fulvescens* (Saussure) and *O. microtis* (J. A. Allen), currently regarded as valid allopatric species occurring north and south of the Amazon, respectively, are difficult to diagnose unambiguously and may be conspecific; new information is provided about the hitherto ambiguous type locality of the latter taxon. (12) *Rhipidomys nitela* Thomas is reported from French Guiana for the first time and its previously unpublished diagnostic differences from other congeners are tabulated and discussed. (13) A lectotype is designated for *Coendou melanurus* (Wagner), and the species is redescribed based on all known specimens in North American and European museums; diagnostic differences between this species and *C. insidiosus* (Olfers) are illustrated for the first time. (14) A red-rumped agouti (*Dasyprocta*) is designated as the neotype of *Mus aguti* Linnaeus to preserve current usage of *Dasyprocta prymnolopha* (Wagler) for the black-rumped agouti. (15) The diagnostic differences between red and green acouchies (*Myoprocta*) are discussed and a neotype is designated for *Cavia acouchy* Erxleben to fix the application of that name to the red species; other nominal taxa of *Myoprocta* are identified as red or green acouchies based on examination of type material and original

descriptions. (16) The diagnostic morphological traits of *Proechimys cuvieri* Petter and *P. guyannensis* (E. Geoffroy) are reevaluated and discussed based on character variation in topotypical (French Guianan) material.

Analyses of our sampling results indicate that distinct sets of nonvolant species are effectively sampled by different inventory methods, and that increased sampling effort with any method generally results in more species. Although the rate of discovery of new species always decreases with increasing sample size, none of our graphs of species accumulation indicate that an asymptotic value was reached with any method. Instead, nonparametric statistical extrapolations suggest that the Paracou nonvolant mammal fauna consists of somewhere between 69 and 74 species; by implication, our nonvolant inventory is about 86–93% complete. Most missing species are probably marsupials and rodents, but one or two expected primate species might have been locally extirpated by hunters prior to our fieldwork.

In terms of higher taxonomic composition, the Paracou nonvolant mammal fauna is typical of those found throughout the humid Neotropical lowlands. However, a quantitative analysis of nonvolant faunal similarity at the species level among 12 exemplar rainforest inventories first clusters the Paracou list with others from the Guiana subregion of Amazonia, next with lists from elsewhere in Amazonia, and lastly with Central American lists. Pairwise similarity values likewise show an obvious positive correlation between faunal resemblance and geographic proximity within the Neotropical rainforest biome. At least 24 species (38%) of the Paracou nonvolant fauna are Amazonian endemics, but 18 (28%) are essentially pan-Neotropical in distribution; the remaining 22 species exhibit a variety of distributional patterns that suggest past connections among different sets of currently disjunct rainforested regions.

Species richness comparisons among nonvolant faunal inventories are complicated by a variety of familiar problems including inconsistent methodology, presence or absence of certain key habitats, and uneven sampling effort. A conservative interpretation of sampling results from La Selva (Costa Rica), Paracou, and Manu (Peru), however, suggests progressive increases in richness of about 23% from Central America to the Guianas, and of about the same amount from the Guianas to western Amazonia; over the entire gradient (Central America to western Amazonia), the net increase in observed richness is at least 50%. Whereas rodents are consistently the most diverse clade in all well-sampled nonvolant faunas, rankings of other orders by relative richness exhibit considerable site-to-site variation, at least some of which appears to reflect real geographic differences in taxonomic diversity rather than sampling artifacts.

Nonvolant rainforest mammals are hard to classify into trophic guilds due to behavioral plasticity and incomplete knowledge of relevant natural history. Preliminary guild comparisons among three exemplar faunas, however, suggest that the Paracou nonvolant community is substantially less diverse in arboreal frugivores and more diverse in terrestrial animalivores than are nonvolant communities at some Central American and western Amazonian sites. Subsistence and recreational hunting has clearly affected local populations of some nonvolant mammals at Paracou; whereas popular game species (e.g., large primates) were seldom sighted, density compensation may explain high local densities of certain other taxa (e.g., *Potus flavus* and *Cuniculus paca*). Patterns of differential habitat use between closely related nonvolant species at Paracou were mostly observed within the terrestrial granivore/frugivore guild.

Combining these results with those previously reported for the sympatric bat fauna, we recorded a total of 142 mammalian species at Paracou. By statistical extrapolation from our sampling data, the entire local community perhaps contains 155–168 species; because the known French Guianan rainforest mammal fauna contains at least 167 species for which suitable habitat is present in our study area, such estimates are plausible. By implication, our inventory is perhaps 85–92% complete overall.

A synthesis of biogeographic information analyzed in this monograph and by Simmons and Voss (1998) suggests that faunal turnover with increasing geographic distance is much higher for nonvolant mammals than for bats, a necessary consequence of observed group differences in endemicity: whereas many nonvolant rainforest mammals have geographic ranges bounded by obvious topographic or habitat discontinuities (e.g., large rivers, xeromorphic vegetation), most rainforest bats are geographically widespread. Not surprisingly, most of the taxa that usefully define a Guianan center of mammalian endemism are nonvolant species. The geographic limits of Guianan endemism appear to be remarkably similar for mammals, birds, snakes, lizards, and trees, suggesting a common pattern of biotic differentiation.

Overall, the Paracou mammal fauna conforms broadly with previous generalizations about community-wide patterns of diel activity and substrate use by Neotropical rainforest mammals, but appears to diverge significantly from conventional views about trophic structure. Whereas there are many more species of secondary consumers than primary consumers at Paracou, primary consumers appear to outnumber secondary consumers by an equally large margin at some western Amazonian inventory sites. Sampling artifacts perhaps explain some of the community differences observed in such comparisons, but real geographic variation in trophic structure is also apparent.

RÉSUMÉ

Ce travail décrit les résultats d'un inventaire de la communauté des mammifères non-volants à Paracou, dans un site de forêts pluvieuses de basse altitude au Nord de la Guyane française. Cette étude complète et conclut l'analyse faunique de cette localité, entamée par la monographie des chauves-souris de Paracou (Simmons et Voss, 1998). En nous limitant à une surface de 3 km de rayon, étudiée durant 202 jours s'étalant de 1991 à 1994, nous avons mis en évidence la présence de 64 mammifères non-volants par la combinaison de différentes méthodes d'echantillonnage: piégeage traditionnel, piégeage en canopée, piégeage par seaux enterrés, chasses diurne et nocturne, et entretiens avec des résidents locaux. Cette communauté comprend 12 espèces de marsupiaux, 9 xénarthres (édentés), 6 primates, 10 carnivores, 5 ongulés, et 22 rongeurs.

Les recherches de systématique comparée effectuées sur les animaux collectés et préservés sous forme de spécimens muséologiques ont permis la découverte de nouveaux taxons, ont documenté l'extension de la répartition géographique d'espèces connues par ailleurs, et ont permis d'aborder et de résoudre plusieurs questions taxonomiques longtemps débattues.

(1) Le petit opossum *Gracilinanus emiliae* (Thomas) est pour la première fois documenté en Guyane; la description de cette espèce est élaborée, et sa distribution géographique connue est documentée. Par comparaison avec la série type et les descriptions originelles, *G. longicaudus* Hershkovitz est considéré comme un synonyme postérieur à *G. emiliae,* mais *Marmosa agricolai* est une espèce différente. (2) Un nouveau genre est proposé pour le taxon *Gracilinanus kalinowskii* Hershkovitz, qui n'était auparavant connu que de l'Est du Pérou, mais qui diffère de tous les autres marsupiaux didelphimorphes par de singuliers caractères morphologiques. (3) *Marmosops parvidens* (Tate) et *M. pinheiroi* (Pine), ce dernier originellement décrit comme une sous-espèce du premier, sont deux taxons distincts, qui vivent en sympatrie à Paracou. Après examen des spécimens de référence (holotype et paratypes), d'autres taxons précédemment mis en synonymie avec *M. parvidens* apparaissent néammoins être des espèces distinctes, comme *M. juninensis* (Tate) et *M. bishopi* (Pine). (4) *Monodelphis brevicaudata* (Erxleben), *M. glirina* (Wagner), et *M. palliolata* (Osgood) sont trois espèces distinctes, reconnaissables par des combinaisons discriminantes de caractères morphologiques. A partir des spécimens à disposition, l'espèce *M. brevicaudata* (dont la localité-type est redéfinie comme Kartabo, au Guyana) apparaît endémique du bouclier guyanais au sein de la région amazonienne, et comporte des formes bi- et tri-colorées. Un néotype de Cayenne (Guyane française) est désigné pour représenter le taxon *Viverra touan* Shaw, qui est le plus ancien nom disponible pour la forme tricolore. (5) *Saguinus midas* (Linnaeus) et *S. niger* (E. Geoffroy), traditionnellement considérés comme synonymes ou comme races conspécifiques, sont reconnaissables de façon indiscutable, et ne semblent pas être des espèces-soeurs; en conséquence de notre analyse, chacun doit être reconnu comme une espèce distincte; un néotype est désigné afin de conserver l'usage répandu du taxon *niger* E. Geoffroy représentant les tamarins aux mains noires du sud-est de l'Amazonie. (6) Deux nouvelles petites espèces du genre *Neacomys* sont décrites à partir du matériel collecté à Paracou et dans d'autres localités de la région des Guyanes; leurs caractères diagnostiques sont documentés par des comparaisons détaillées avec d'autres congénères de taille similaire vivant en régions septentrionales d'Amérique du Sud. (7) *Nectomys melanius* Thomas est reconnu comme une espèce distincte des taxons *N. squamipes* (Brants) et *N. palmipes* J. A. Allen et Chapman. Cependant, *N. parvipes* Petter n'est pas un taxon valide, et est mis ici en synonymie avec *N. melanius.* (8) Les caractères diagnostiques de *Neusticomys oyapocki* (Petter et Dubost), une espèce jusqu'ici connue par le seul holotype, sont discutés et illustrés à partir de nouveaux spécimens récemment collectés. (9) *Oecomys*

auyantepui Tate et *O. paricola* (Thomas), auparavant mis en synonymie, sont différentes espèces reconnaissables par des caractères craniens discriminants; ces taxons ont des répartitions allopatriques, respectivement au Nord et au Sud de l'Amazone. (10) Un examen détaillé des petits spécimens d'*Oecomys* provenant de Paracou et d'autres localités de la région des Guyanes confirme l'interprétation d'autres auteurs comme quoi *O. rutilus* Anthony et *O. bicolor* (Tomes) sont des espèces distinctes, discrètement mais clairement reconnaissables. (11) La diagnose et la distinction d'*Oligoryzomys fulvescens* (Saussure) et *O. microtis* (J. A. Allen), actuellement considérées comme espèces allopatriques distribuées respectivement au Nord et au Sud de l'Amazone, sont difficiles à établir, et ces deux taxons pourraient être conspécifiques; de nouvelles données sont apportées au sujet de la localité-type d'*O. microtis,* dont l'emplacement était jusqu'alors ambigu. (12) *Rhipidomys nitela* Thomas est signalé pour la première fois de Guyane française, et les différences morphologiques diagnostiques de cette espèce sont présentées et discutées par rapport aux autres espèces du genre. (13) Un lectotype est désigné pour l'espèce *Coendou melanurus* (Wagner), et la description de ce taxon est détaillée à partir des spécimens connus dans les musées nord-américains et européens. Des comparaisons et diagnoses par rapport à *C. insidiosus* (Olfers) sont effectuées pour la première fois. (14) Un spécimen d'agouti à croupion rouge (genre *Dasyprocta*) est désigné comme néotype du taxon *Mus aguti* Linnaeus, afin de préserver l'usage du nom *Dasyprocta prymnolopha* (Wagler) pour les agoutis à croupion noir. (15) Les différences caractéristiques des acouchis rouge et olive du genre *Myoprocta* sont discutées; un spécimen collecté à Paracou est désigné comme le néotype de *Cavia acouchy* Erxleben, afin de pouvoir appliquer ce nom à l'acouchi rouge. D'autres taxons du genre *Myoprocta* sont identifiés comme appartenant aux groupes des acouchis rouges ou olives, à partir du matériel des localités-type et des descriptions originelles. (16) Les caractères morphologiques permettant de discriminer les espèces *Proechimys cuvieri* Petter et *P. guyannensis* (E. Geoffroy) sont ré-évalués et discutés à partir de l'examen de la variation de ceux-ci parmi des spécimens topotypiques de Guyane française.

Les analyses qualitative et quantitative de nos efforts de collecte indiquent que différents ensembles de mammifères non-volants sont mis en évidence par les différentes techniques d'observations et de captures. En général, un effort d'échantillonnage accru conduit à détecter un plus grand nombre d'espèces, quelle que soit la technique considérée. Bien que le taux de découverte de nouvelles espèces décroisse au fur et à mesure des efforts cumulés, l'examen des courbes d'accumulation de taxons indique qu'aucune de nos méthodes n'a permis d'atteindre une valeur d'asymptote. Plus précisément, des extrapolations utilisant des statistiques non-paramétriques suggèrent que la communauté des mammifères non-volants de Paracou renferme de 69 à 74 espèces. Cette prédiction implique que notre inventaire ne représenterait que 86 à 93% des espèces potentiellement présentes. La plupart des espèces non-détectées sont probablement des marsupiaux et des rongeurs, mais l'un ou l'autre primates absents de nos inventaires ont peut-être été récemment éliminés de la zone d'étude par une chasse trop excessive.

En ce qui concerne la composition taxonomique des familles et des ordres, la faune des mammifères non-volants de Paracou est bien représentative de celles connues dans d'autres zones de plaine (forêts ombrophiles) des Néotropiques. Cependant, une analyse quantitative, au niveau des espèces partagées, des similarités entre 12 localités forestières néotropicales où des inventaires comparables ont été effectués, indique que la faune de Paracou se regroupe avec d'autres inventaires de la région des Guyanes, puis avec des listes fauniques d'autres régions amazoniennes, et enfin avec des peuplements d'Amérique centrale. Ainsi, les indices de similarité d'une matrice d'espèces partagées montrent une corrélation positive entre les similarités de faune et la proximité géographique au sein du biome que sont les forêts humides néotropicales. Au moins 24 espèces (soit 38% de notre inventaire) de la faune (à l'exclusion des chiroptères) de Paracou sont des endémiques de l'Amazonie, mais 18 (28%) ont une large répartition pan-néotropicale; les 22 espèces restantes présentent différents patrons de distribution qui suggèrent d'anciennes connections entre les ensembles forestiers sud-américains actuellement discontinus.

Toutefois, il faut admettre que les comparaisons, en terme de richesses d'espèces, entre les différents inventaires de mammifères non-volants sont biaisées par divers problème inhérents à ces études: méthodologies non strictement comparables, absence ou présence de certains habitats singuliers, et inégalités des efforts de collecte. Néammoins, une interprétation prudente des données d'inventaires de trois localités, La Selva (Costa Rica), Paracou et Manu (Pérou),

suggère un accroissement progressif de la richesse en espèces d'environ 23% entre l'Amérique Centrale et les Guyanes, et d'environ la même ampleur entre les Guyanes et l'Amazonie occidentale. Sur l'ensemble du gradient "Amérique centrale → Guyanes → Amazonie occidentale", l'augmentation des biodiversités observées est d'au moins 50%. Alors que les rongeurs représentent le taxon le plus diversifié dans toutes les études basées sur des inventaires approfondis, l'abondance relative des autres ordres de mammifères non-volants diffère profondément selon les sites examinés. Dans certains cas, l'abondance ou la rareté d'un ordre particulier semble refléter de réelles différences géographiques au travers des forêts amazoniennes, et non pas des artefacts d'échantillonnages.

Les mammifères non-volants des forêts humides sont difficilement classables en guildes trophiques du fait d'une part de leur plasticité comportementale et d'autre part du manque de connaissances quant à leurs traits d'histoire de vie. Nous présentons néammoins des comparaisons préliminaires, basées sur trois faunes particulièrement bien documentées, qui suggèrent que la communauté de Paracou est moins riche en frugivores arboricoles et plus diverse en animalivores terrestres par rapport aux communautés d'Amérique centrale et d'Amazonie occidentale. La chasse, qu'elle soit de subsistance ou de loisirs, a clairement modifié la communauté des mammifères de Paracou, éradiquant les populations locales de certaines espèces. Ainsi, les espèces-gibiers les plus recherchées (comme les grands primates) ont été rarement observées, alors que des phénomènes de compensation pourraient expliquer les densités relativement élevées d'autres taxons (par exemple, *Potos flavus* et *Cuniculus paca*). Enfin, nos observations suggèrent un usage différent des habitats par des espèces apparentées, ce qui a été noté à Paracou principalement au sein de la guilde des mammifères terrestres granivores-frugivores.

En réunissant ces résultats avec ceux acquis précédemment pour la faune des chauves-souris de Paracou, nous avons donc mis en évidence l'existence de 142 espèces dans cette localité de Guyane française. Par des extrapolations statistiques de nos données d'échantillonnage, nous estimons que la communauté locale renferme probablement de 155 à 168 espèces. Comme la faune des mammifères forestiers de Guyane renferme au moins 167 espèces dont l'habitat, tel que nous le connaissons, est représenté à Paracou, notre estimation semble réaliste. Ces considérations impliquent que nos inventaires, concernant tant les chauves-souris que les mammifères non-volants, auraient mis en évidence de 85 à 92% des espèces présentes.

Une synthèse des informations biogéographiques analysées dans ce travail et dans celui de Simmons et Voss (1998) suggère alors que les changements de faune (renouvellement faunique, ou "faunal turnover"), en rapport avec l'éloignement géographique, sont beaucoup plus marqués pour les mammifères non-volants que pour les chauves-souris, une conséquence liée aux différences d'endémicité caractérisant ces deux groupes d'animaux. En effet, tandis que de nombreux mammifères forestiers non-volants ont des répartitions géographiques circonscrites par des discontinuités topographiques ou écologiques (grands fleuves, végétation xéromorphe), la plupart des chauves-souris des forêts néotropicales humides sont largement répandues dans l'espace. Il s'ensuit que la plupart des taxons qui pourraient définir de façon claire un endémisme au niveau des Guyanes sont des mammifères non-volants. Nous relevons aussi que les limites géographiques de l'endémisme des Guyanes apparaissent très semblables pour divers organismes, mammifères, oiseaux, serpents, lézards, et arbres, suggérant un patron commun de différentiation pour ce biome.

En conclusion, la faune des mammifères de Paracou reflète bien, en tant qu'exemple concret, les enseignements des ouvrages généraux en ce qui concerne les patrons d'activité journalière et d'utilisation des substrats et des habitats par les mammifères forestiers néotropicaux, mais une différence d'importance, par rapport à la littérature, concerne la structure trophique. Alors qu'il y a beaucoup plus d'espèces de consommateurs secondaires que primaires à Paracou, les consommateurs primaires sont au contraire plus nombreux, par un nombre d'espèces tout aussi important, dans certains sites étudiés en Amazonie occidentale. Bien qu'il soit possible que des biais d'échantillonnage soient responsables de certaines différences observées entre ces communautés, il n'en reste pas moins qu'une importante variation géographique existe quant à la structure et à la composition des niches trophiques des mammifères habitant les forêts néotropicales humides.

INTRODUCTION

This report is the second and concluding part of our monographic treatment of the mammal fauna of Paracou, a rainforested locality in the coastal lowlands of northern French Guiana (fig. 1). In the first part (Simmons and Voss, 1998) we outlined the overall goals of our inventory project, described our study site, explained the methods we used to sample local bat diversity, summarized our systematic research with collected bat voucher material, and analyzed our bat-sampling results. Herein we provide comparable information about the nonvolant species, provide a synthetic overview of Paracou mammal diversity, compare our whole-faunal sampling results with those from other inventory sites, and evaluate the prospects and priorities for future mammalian diversity research in the rainforested Neotropical lowlands.

NONVOLANT MAMMAL INVENTORY METHODS

Nonvolant mammals are so variable in size and behavioral traits that capture equipment or observational methods suitable for some taxa may be entirely ineffective for others (Voss and Emmons, 1996). Additionally, whereas some taxa or ecological guilds are minimally affected by human activities, others can be extirpated by overhunting even in extensive tracts of uncut forest. To an even greater extent than in our bat survey (Simmons and Voss, 1998), we therefore relied on a combination of methods to inventory nonvolant mammal diversity at Paracou.

Conventional Trapping

We used standard trapping equipment (Voss and Emmons, 1996) to sample the local fauna of small marsupials and rodents near ground level during our 1991 and 1992 field seasons. Most traplines included both Victor rat traps (with push-down wooden bait pedals) and folding aluminum Sherman live traps (measuring 80 × 90 × 230 mm) set at approximately 20-m intervals along existing trails through our study area (fig. 2). Because our objective was to sample the fauna as effectively as possible, no attempt was made to randomize or standardize the placement of traps. Instead, traps were placed to maximize capture success for the widest range of anticipated species as suggested by prior experience in other habitats and at other rainforested localities. Victor rat traps were sometimes set on the ground (often inside the dark cavities of hollow logs), but we usually tied them to lianas, tree trunks, and other woody supports 0–2 m above the ground to capture semiarboreal species (fig. 3, top). Sherman traps were usually placed on the ground next to fallen trunks, under large-leaved vegetation (palms, heliconias, etc.), beneath viny tangles and piled branches, or in similarly sheltered terrestrial situations (fig. 3, bottom).

Victor rat traps were usually baited with a ground-up mixture of peanut butter, raisins, rolled oats, and bacon (in 6:2:2:1 proportion); although this bait effectively attracts many species of small mammals, it also attracts ants and must be renewed daily in most situations. Sherman live traps were baited daily with either cracked corn (sold locally as chicken feed) or with commercial birdseed; both baits were effective when dry, but cracked corn becomes sticky when wet and subsequently spoils unless the trap is washed. Traplines were checked twice daily, usually at dawn and in the late afternoon (between 16:00 and 18:30 hours). All traps were rebaited in the late afternoon. Sherman traps were disassembled, thoroughly washed (without soap), and dried after each capture to remove urine, feces, and old bait. The treadles of Victor traps were scraped clean of old bait at each rebaiting, but the traps themselves were not washed. We marked all trap locations with brightly colored vinyl surveyor's tape, and all Victor traps were tethered to nearby stems or roots with a short (ca. 80 cm) length of braided cotton or nylon cord.

Most trapped trails traversed both well-drained and swampy primary forest, the two principal habitat types sampled by this method. In addition, a few traplines were set for semiaquatic species by wading small streams and setting traps along the banks, and some traps were set in the secondary vegetation bordering our camp clearing and nearby roads. We did not trap in the coastal savannas north of our study area.

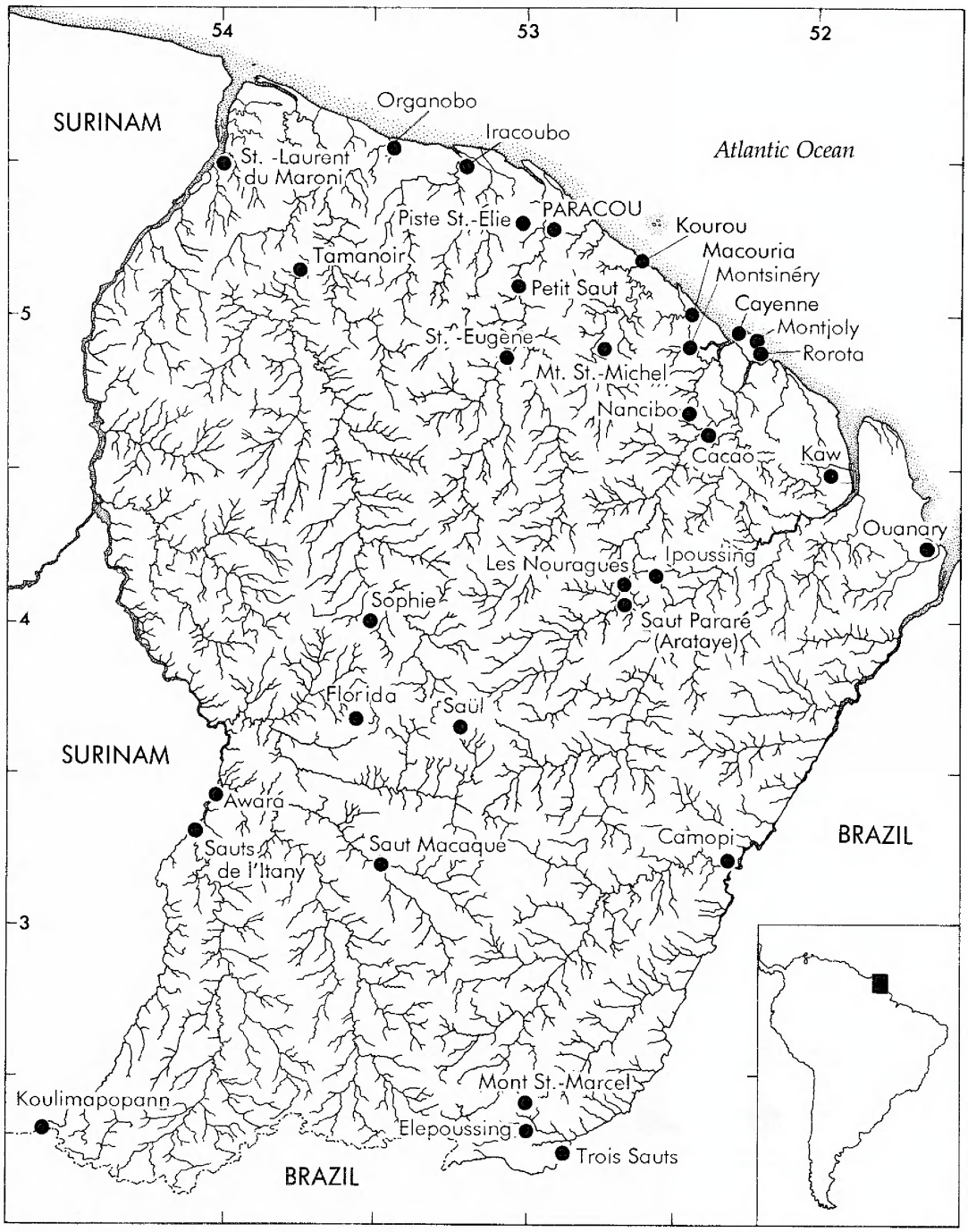

Fig. 1. Map of French Guiana showing the location of our study site at Paracou in relation to other places mentioned in the text. Localities that we could not associate with unique geographic coordinates (e.g., "Rivière Approuague") are not shown. One degree of latitude or longitude is approximately equal to 110 km.

Fig. 2. Trail through well-drained primary forest sampled by trapping and hunting at Paracou. Most traps were set within a few meters of such narrow paths, which do not materially alter the habitats they traverse.

Fig. 3. Two standard traps as typically deployed to sample nonvolant mammal diversity near ground level. **Top,** Victor rat trap tied to liana. **Bottom,** Sherman live trap on the ground. Sixteen species of small marsupials and rodents were taken in mixed Victor/Sherman traplines at Paracou.

We periodically used Tomahawk folding wire live traps (measuring 145 × 145 × 410 mm) to capture large (>300 g) terrestrial marsupials and rodents (fig. 4). Most Tomahawk traps set on the ground were baited with coconut or ripe plantain, and a few unbaited large Tomahawks (measuring 250 × 300 × 810 mm) were set in streams for semiaquatic species. We used small leghold traps and Conibear break-back traps with and without bait or commercial scent lures in 1991, but not in subsequent field seasons; most of these traps were set away from established trails, often in burrows or on logs crossing small streams. In 1992 we also constructed and field-tested two live traps designed for use in armadillo tunnels, but these were unsuccessful and the effort was discontinued in subsequent years.

Arboreal Trapping

Because some species of rainforest marsupials and rodents seldom descend from the canopy or subcanopy, we used a platform-trapping system similar to that described by Malcolm (1991) to capture arboreal species in 1993. Trees were climbed using French pole climbers (see Mori, 1987: fig. I-3A), of which a small pair with a maximum tooth-to-tooth span of 25 cm and a larger pair spanning 35 cm were useful for climbing boles of different diameters. Wooden platforms provided with eyelets for raising and lowering trap assemblies by nylon lines were nailed to tree trunks 7–19 m above the ground in both well-drained and swampy primary forest. Each trap assembly consisted of one Tomahawk folding wire live trap (measuring 145 × 145 × 410 mm) and one piggybacked Sherman folding aluminum live trap (measuring 80 × 90 × 230 mm) attached to a wooden frame (fig. 5). Sherman traps were baited with the same oatmeal/peanut/raisin/bacon mixture described previously, and the Tomahawk traps were baited with pieces of coconut and ripe plantain; bait was renewed as necessary, about every three to four days on average. Tree traps were checked daily soon after dawn with binoculars.

Pitfall Trapping

Many species of small terrestrial mammals are not attracted to baited traps, so we used a pitfall trapping design suggested by S. M. Goodman (personal commun.) to supplement our conventional trapping in 1993. We used 15-liter plastic buckets as pitfalls, and sunk these flush with the ground in linear series beneath sheet-plastic drift fences (fig. 6). Each pitfall trapline consisted of 11 buckets spaced 5 m apart, with one bucket at either end, for a total length of 50 m. Drift fences, consisting of a continuous barrier running the entire length of each trapline, were made of 50-cm-wide strips of heavyweight (6 mil) clear polyethylene stapled to vertical stakes hammered into the ground every 3–4 m. A broad (7–8 cm) fold of plastic was heaped with soil to anchor the bottom of the fence, and a flap was cut in this fold where it passed over each bucket.

We perforated the bottoms of the buckets so that rainwater could drain out, but the perforations soon became clogged and we then noticed that undrained buckets containing 10–15 cm of water were much more effective traps than dry buckets. Thereafter, we added water to all of the buckets and tried to maintain this level throughout our pitfall-trapping effort. Most captured animals drowned in pitfalls containing water, but checking the traplines twice daily was sufficient to prevent specimen damage due to decomposition.

Hunting and Sight Surveys

We relied on hunting, sight surveys, and interviews (see below) to census the local fauna of large mammals (≥1 kg) that were difficult or impossible to capture with our trapping equipment. However, we seldom hunted or made sight surveys in the daytime because mornings were occupied by checking traplines, taking down bat nets, or preparing specimens, and afternoons were usually spent rebaiting traps or setting up bat nets. Most of our personal observations of diurnal mammals at Paracou were therefore made haphazardly in the course of other (relatively noisy) activities. Fortunately, local forestry workers were familiar with most species of large diurnal mammals known or expected to occur in the area, so interviews compensated to some extent for the deficiencies of our diurnal census effort.

Fig. 4. Tomahawk folding wire live trap as typically deployed to supplement Victor- and Sherman-trapping near ground level.

By contrast, we regularly hunted at night, and we recorded many sightings of nocturnal species encountered by deliberate searching. Equipped with notebook, shotgun, and a nine-volt headlight with focusable reflector, we walked slowly (about 0.5–1.5 km/hour) along established trails scanning the vegetation with the headlight reflector adjusted to produce a moderately broad beam. When eyeshine was detected, we narrowed the beam to give brighter illumination; binoculars were sometimes used to identify animals revealed by eyeshine in the canopy or subcanopy. Most of our nocturnal surveys were made in the early evening (between 19:00 and 24:00 hours), but we also hunted between midnight and dawn on many nights. Some nonvolant species were observed in the course of bat netting, especially large marsupials attracted to the squeals of captured bats.

Specimens were collected by shooting with side-by-side 20-gauge shotguns. We used commercial 20-gauge game loads for large mammals, but small mammals were collected with .410 or .22 caliber shot-shells loaded in removable auxilliary barrels (''auxes'') machined from brass rod stock. Most unvouchered sightings of small marsupials and rodents could not be confidently identified to species.

Interviews

Small teams of day laborers have been continuously employed in forestry research projects at Paracou since the mid-1980s to cut trails, clear experimental plots, and to mark and measure tens of thousands of trees. Among these workers are members of the Saramaka and Boni tribes of so-called bush negroes, descendants of escaped slaves (maroons) who fled into the forests of Surinam and French Guiana and re-created traditional African communities that have resisted acculturation for centuries (Kahn, 1931; Hurault, 1961; Price, 1976). Recruited for their ability to identify commercially valuable timber, these people have observed (and hunted) the Paracou fauna for many years. We periodically discussed our inventory work with them, comparing our own observations with

Fig. 5. Arboreal platform trap assembly in place at Paracou. Modified from Malcolm's (1991) basic design, each trap assembly consisted of one folding wire Tomahawk trap and a piggy-backed folding aluminum Sherman trap. Both are visible in this photograph, which resembles the perspective of an observer on the ground checking the traps with binoculars. Six species of marsupials and rodents were taken with this equipment, at heights ranging from 7.2 to 16.7 m above the ground.

theirs and asking them about species we had not yet seen. Most of our useful interview data, however, was obtained from conversations with their French-born foreman, Pascal Petronelli, himself a gifted naturalist and a local resident since 1983.

Using distributional data summarized for another study (Voss and Emmons, 1996), we compiled a list of the nonvolant mammal species known or expected to occur in French Guiana, and we used this list as the basis for interviewing Mr. Petronelli in 1993. We focused primarily on large species ($\geq$1 kg) that nonmammalogists might reasonably be expected to recognize without special effort, but we also asked about a few smaller species identifiable by obvious external characters. For each species expected to occur in the area but not observed by us, we asked if he had seen it himself, or whether the species had been seen by the forestry workers he supervised. If the species had been seen, we asked for details about where and when the sighting(s) occurred, and about distinguishing morphological or behavioral characteristics; we often used the illustrations in Emmons (1990) to discuss diagnostic differences among related species. For some species, we were able to examine photographs and/or written records (logs of noteworthy sightings on experimental plots). Finally, we asked Mr. Petronelli if any species not mentioned by us had ever been seen in the area.

Previous Mammalogical Research at Paracou

Whereas information about bat diversity at Paracou (summarized by Simmons and Voss, 1998) derived entirely from our own efforts, other researchers had previously worked on the local nonvolant mammal fauna prior to our study (Dubost, personal commun.; Forget, 1991, 1996, 1997; Henry, 1994, 1996,

Fig. 6. Detail of a pitfall trapline installed beneath a sheet-plastic drift fence at Paracou. Loose soil (excavated to sink the pitfalls) is heaped along a broad bottom fold of plastic to anchor the base of the drift fence; the remaining plastic is stapled to upright stakes for support. Twelve species of small marsupials and rodents were taken by this method at Paracou, in addition to amphibians, squamate reptiles, and arthropods.

1999; Forget et al., 1999). Their published results and unpublished observations provided supplementary information about local diversity, including records of three species that neither we nor our resident interviewees had identified. Of particular importance was the very large series of specimens trapped over several years by O. Henry, which we were generously allowed to inspect (through the good offices of L. Granjon) for taxa unrepresented in our voucher collection.

Voucher Preservation

We preserved voucher material of nonvolant species following standard protocols (e.g., Nagorsen and Peterson, 1980; Hall, 1981). As explained previously (Simmons and Voss, 1998: 19–21), our primary motivation in preserving voucher material was to obtain enough material from each species to assess the taxonomic status of the Paracou population with respect to museum samples from other Neotropical localities. Additionally, our voucher collection (now divided between the AMNH and the MNHN) provides a permanent archive of mammalian diversity at Paracou that can be consulted by other zoologists, who may confirm or emend our identifications in the light of future taxonomic revisions.

Nevertheless, we only collected voucher material for small species (few of which could otherwise be identified with confidence) and for some large mammals judged to be sufficiently abundant that removal would not significantly affect the local population. In general, samples consisting of about 10 adult males and 10 adult females are sufficient to obtain meaningful estimates of the mean and range of variation in each sex for characters of taxonomic interest, and our voucher series only exceed these minimal counts for a few of the commonest marsupials and rodents (e.g., *Didelphis marsupialis, Philander opossum, Oryzomys megacephalus, Proechimys cuvieri*). For open populations of most small nonvolant species, collecting on this scale is probably trivial by comparison with natural demographic processes.[1]

[1] Demographic data on small nonvolant tropical mammals are hard to come by, but Fleming's (1971) study of *Proechimys semispinosus* in Panamanian lowland forests provides some basis for inference. His estimates of median density (300 individuals per square kilometer) and annual survivorship (36%) suggest that ecologically similar taxa such as *P. cuvieri* or *P. guyannensis* could maintain local populations of about 8400 individuals in our study area (28 km^2; Simmons and Voss, 1998), of which almost 5400 would be expected to die annually of natural causes.

SYSTEMATIC ACCOUNTS

A significant difference in the scope of taxonomic problems encountered in working up the bats and the nonvolant mammals from Paracou accounts for certain format differences between the systematic accounts below and those in Simmons and Voss (1998). Whereas most of the bat genera represented in the Paracou fauna have been revised taxonomically in the last half-century, very few revisions are available to facilitate the identification of nonvolant taxa. Furthermore, many of the unrevised nonvolant taxa in the Paracou fauna were first described by Linnaeus and other early zoologists, who often named species based on subsequently misplaced specimens, or on the unvouchered descriptions of even earlier travellers. Most of these names have been sources of taxonomic confusion for centuries, and it was found impossible to use them unambiguously without resolving difficult problems of conflicting usage. To do so, we examined types and other relevant material from many museums, and we now designate lectotypes or neotypes as necessary to fix the application of problematic names. For some species that lacked published syntheses of geographic data, we tried to examine every known specimen in order to map distributions for this report.

Because taxonomic problems of varying complexity were encountered in working up the nonvolant fauna, the organization of these accounts differs from species to species. Nevertheless, we tried to maintain some consistency in the order in which information is presented. Whether or not subheadings are used, we first list the specimens or observations that provide evidence for the species at Paracou. Next, we discuss issues of identification. For species that can be unambiguously identified with standard references, only a brief comment to that effect is necessary, but many species required more extensive treat-

ment for the reasons just explained. Field observations are summarized last.

Where formal taxonomic treatment is required, either for the description of new species or to resolve complex issues of usage, we use as many as six subheadings (Type Material, Distribution, Description, Comparisons, Remarks, Other Specimens Examined) to organize relevant information. Wherever possible, we attempted to sequester information about nomenclature under the heading "Remarks". Under "Other Specimens Examined" we list the additional material (besides Paracou vouchers) on which our systematic conclusions are based.

All linear measurements cited or tabulated below are in millimeters (mm). External measurements and weight of individual specimens are given in the text according to the formula: Length of Head-and-Body (HBL) × Length of Tail (LT) × Length of Hindfoot (HF) × Length of Ear (Ear), followed by weight (Wt) in grams (g) or kilograms (kg). Length of Head-and-Body was obtained by subtracting Length of Tail (basal flexure to fleshy tip) from Total Length (nose to fleshy tail-tip); Length of Hindfoot includes the claws; and Length of Ear was measured from the notch (see Husson, 1978: fig. 1). Unless otherwise noted, external measurements and weights are those recorded by collectors in the field (or were calculated from the collector's measurements as described above for Head-and-Body Length). Craniodental measurements are defined elsewhere in the text. We tabulate the sample mean plus or minus one standard deviation, the observed range, and the sample size (N) for $N \geq 10$ specimens; only the sample mean, the observed range, and the sample size are tabulated for $N < 10$ specimens.

Voucher material from Paracou is deposited in the American Museum of Natural History, New York (AMNH), and in the Muséum National d'Histoire Naturelle, Paris (MNHN). Other specimens cited below are in museums identified by the following acronyms:

AC	Muséum d'Anatomie Comparée (Paris)
BMNH	Natural History Museum (London)
CM	Carnegie Museum of Natural History (Pittsburgh)
EBRG	Estación Biológica de Rancho Grande (Maracay)
FMNH	Field Museum of Natural History (Chicago)
INPA	Instituto Nacional de Pesquisas da Amazônia (Manaus)
KU	University of Kansas Museum of Natural History (Lawrence)
MHNG	Muséum d'Histoire Naturelle de Genève (Geneva)
MHNLS	Museo de Historia Natural La Salle (Caracas)
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima)
MVZ	Museum of Vertebrate Zoology University of California (Berkeley)
NMW	Naturhistorisches Museum Wien (Vienna)
RMNH	Rijksmuseum van Natuurlijke Historie (Leiden)
ROM	Royal Ontario Museum (Toronto)
UG	University of Guyana (Georgetown)
USNM	National Museum of Natural History (Washington, D.C.)
UZM	Universitets Zoologiske Museum (Copenhagen)
V-	Institut des Sciences de l'Évolution (Montpellier)
ZMB	Museum für Naturkunde der Humboldt-Universität zu Berlin (Berlin)

Marsupialia

Twelve species of marsupials, all traditionally classified in the family Didelphidae,[2] are known to occur at Paracou, and two additional species could be expected to occur locally (see appendix 1). Our terminology for most qualitative aspects of marsupial morphology follows Archer (1976a, 1976b) and

[2] An alternative classification proposed by Hershkovitz (1992) would assign the Paracou marsupial genera to several different families: Marmosidae (*Gracilinanus, Marmosa, Marmosops, Metachirus, Micoureus, Monodelphis*), Caluromyidae (*Caluromys*), and Didelphidae (*Chironectes, Didelphis, Philander*). Morphological support for caluromyid and marmosid monophyly is weak, however, and available molecular data consistently support other generic groupings (Patton et al., 1996; Palma and Spotorno, 1999; Jansa and Voss, 2000). In the absence of a well-corroborated phylogenetic classification of New World marsupials, we continue the traditional usage of Didelphidae to include the entire didelphimorph crown group.

Hershkovitz (1992, 1997), but we adhere to the traditional interpretation of postcanine dental homologies (Flower, 1867; Luckett, 1993), wherein the replaced molariform tooth of the upper and lower jaw is the deciduous third premolar (dP3/dp3). Thus, the adult didelphid dental formula is I 5/4, C 1/1, P 3/3, M 4/4). We define specimens to be *juvenile* if dP3 is still in place, *subadult* if dP3 has been shed but P3 and/or M4 are still incompletely erupted, and *adult* if the permanent maxillary dentition is complete.

Our quantitative comparisons of marsupial crania are based on the following measurements (fig. 7):

Condylobasal Length (CBL): From the occipital condyles to the anteriormost point of the premaxillae.

Maxillary Toothrow (MTR): Crown length, from the anterior margin of the canine to the posterior margin of M4.

Molar Length (LM): Crown length of M1–4, measured on the labial side of the toothrow.

Palatal Breadth (PB): Measured across the labial extremes of the crowns of the last molars.

Palatal Length (PL): Measured in the midline from the anteriormost point of the premaxillae to the end of the palate.

Nasal Breadth (NB): Measured across the triple-point suture of the nasal, frontal, and maxillary bones on each side.

Least Interorbital Breadth (LIB): Measured at the narrowest point across the frontals between the orbits.

Least Postorbital Breadth (LPB): Measured at the narrowest point across the frontals behind the orbits.

Zygomatic Breadth (ZB): Greatest breadth across the zygomatic arches.

A few other craniodental measurements taken for special purposes are either self-explanatory or are defined in the following species accounts. Because most didelphids exhibit obvious sexual size dimorphism, we summarize morphometric variation separately by gender.

Most of the large opossums in the Paracou fauna (*Caluromys, Chironectes, Didelphis, Metachirus, Philander*) are easily distinguished, even at a distance, by external characters described by Emmons (1990, 1997). However, all of the "marmosine" opossums (species of *Gracilinanus, Marmosa, Marmosops,* and *Micoureus*; formerly placed in the genus *Marmosa* sensu Tate, 1933) require specimens in the hand for positive identification, and some cannot be confidently distinguished without cleaned cranial material. Husson (1978) provided a useful key to Surinamese marsupials based on craniodental characters, but four species now known to occur in Surinam and/or French Guiana were omitted: *Didelphis albiventris, "Gracilinanus" kalinowskii, Marmosops parvidens,* and *Marmosops pinheiroi.* Distinguishing morphological characteristics of these recently reported members of the eastern Guianan fauna are described and illustrated in the accounts that follow.

Caluromys philander (Linnaeus)

VOUCHER MATERIAL: AMNH 266402, 266408, 266409, 267330, 267331, 267333–267337; MNHN 1995.884–1995.886, 1995.894, 1995.902. Total = 15 specimens (not including pouch young).

IDENTIFICATION: Our material agrees closely in external and craniodental characters with Husson's (1978) detailed description of topotypic specimens from Surinam, and measurements of adult Paracou vouchers (table 1) broadly overlap those of topotypic adults (op. cit.: table 1).

In view of the fact that *Caluromys* has never been revised, it is noteworthy that published measurements of some nominal taxa currently regarded as synonyms of *C. philander* (see Gardner, 1993) fall outside the known range of variation among Surinamese and French Guianan specimens. In particular, specimens from Trinidad and northern Venezuela formerly referred to *C. trinitatis* Thomas (type locality: "Botanic Gardens, Trinidad") are substantially smaller and differ from typical *philander* in coloration (Thomas, 1894, 1903, 1904; Pérez-Hernández et al., 1994). Furthermore, we have personally observed conspicuous variation in size and pelage traits among populations currently referred to *C. philander* from Amazonian Brazil. Although Cabrera (1958) recognized *C. p. philander* (including *trinitatis* as a synonym), *C. p. affinis* (type locality:

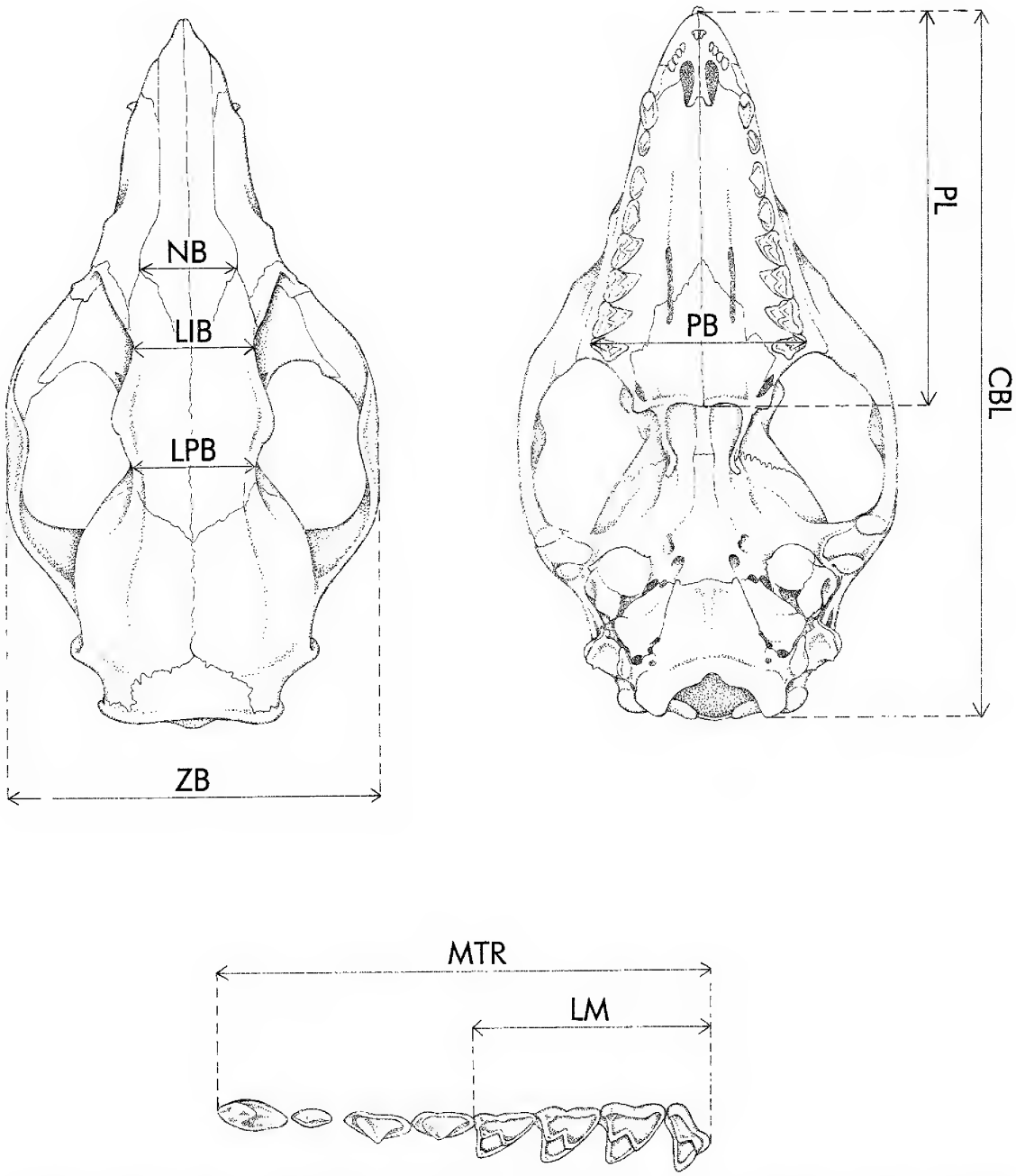

Fig. 7. Dorsal and ventral views of the skull, and occlusal view of the maxillary dentition of *Marmosa murina,* showing the anatomical limits of marsupial measurements defined in the text.

Mato Grosso, Brazil), and *C. p. dichrurus* (type locality: "Ypanema", São Paulo, Brazil) as valid subspecies, the empirical basis for a trinomial nomenclature has never been established. The material now available to evaluate geographic variation and subspecies (or species) limits within what might be called the *Caluromys philander* complex is too large to review in this faunal report, but from the close similarity noted above between Surinamese and French Guianan material it seems clear that the Paracou popu-

TABLE 1
Measurements (mm) and Weights (g) of Adult *Caluromys philander* from Paracou

	AMNH 266409	AMNH 267336	AMNH 267337	MNHN 1995.884	AMNH 267335	MNHN 1995.885	MNHN 1995.894
Sex	male	male	male	male	female	female	female
HBL	271	224	243	274	276	279	263
LT	373	373	405	387	410	383	402
HF	43	44	46	44	42	43	43
Ear	37	35	36	40	38	36	36
CBL	56.7	54.8	57.1	57.8	58.7	—	56.2
LM	9.7	9.7	9.6	10.2	9.9	10.2	9.5
PB	17.1	16.8	17.2	17.3	16.7	17.4	17.2
PL	30.2	30.2	30.6	30.9	32.3	—	31.1
LIB	9.2	8.6	10.0	10.6	9.4	9.1	9.1
ZB	32.9	31.0	33.5	34.3	33.2	34.2	33.4
Wt	352	220	345	345	390	330	325

lation is referable either to the nominate subspecies (if a trinomial nomenclature is warranted) or to *C. philander* sensu stricto (if additional species are recognized in this group).

FIELD OBSERVATIONS: All of our 15 vouchered records of *Caluromys philander* at Paracou are from specimens trapped or shot at night in trees in primary forest, at both well-drained and swampy sites. In addition, we recorded three unvouchered nocturnal observations of this species, two of which were sighted in trees in roadside secondary growth and the third on a liana in primary forest. Seven (47%) of our vouchers were obtained by shooting animals sighted in the forest canopy or subcanopy, and eight others (53%) were taken in subcanopy platform traps. Measured heights above the ground for the trapped specimens ranged from 12 to 16 m, whereas visually estimated heights of sightings of free-ranging (untrapped) animals ranged from 3 to 20 m. Figure 8 provides a typical view of the subcanopy habitat of this species at Paracou.

All four of our adult female vouchers were carrying suckling young. The first, captured on 10 August 1991, had three nursing young measuring 36 mm crown-rump; the second, taken on 14 August 1991, had five young measuring 47 mm crown-rump; the third, taken on 16 November 1992, had two young measuring 14 mm crown-rump; and the fourth, taken on 28 August 1993, had four young measuring 54 mm crown-rump. With these exceptions, all of our vouchered and unvouchered records of *Caluromys philander* are based on solitary individuals; no others were trapped or sighted together.

Chironectes minimus (Zimmermann)

VOUCHER MATERIAL: AMNH 266477, 266478; MNHN 1998.672. Total = 3 specimens.

IDENTIFICATION: Our voucher material conforms closely to most published descriptions of this widespread and distinctive species (e.g., Thomas, 1888; Cabrera, 1919; Krumbiegel, 1940a; Augustiny, 1942; Mondolfi and Medina, 1957; Husson, 1978; Marshall, 1978b; Emmons, 1990, 1997), but a few discrepancies and supplementary observations merit comment. Persistent references (op. cit.) to brownish and yellowish tints in the pelage of *Chironectes minimus* are probably based on old (faded or stained) museum skins; living animals and fresh skins have clear black-and-gray dorsal markings and pure white venters, with no trace of other hues. According to Cabrera (1919), the digits of the manus are webbed to the ends of the first phalanges, but our specimens (and those illustrated by Augustiny [1942: fig. 14] and Mondolfi and Medina [1957: fig. 1]) have unwebbed manual digits. The "supernumerary facial bristles" mentioned by Marshall (1978b) are the usual superciliary, genal, and

Fig. 8. Subcanopy habitat of *Caluromys philander* and other arboreal mammals (e.g., *Micoureus demerarae, Potos flavus, Oecomys rutilus, O. auyantepui, Rhipidomys nitela*) sampled by platform-trapping and by hunting at Paracou.

interramal vibrissae (Brown, 1971), which are well developed (Augustiny, 1942: fig. 11) but otherwise unremarkable in *C. minimus.* Apparently, the only postcranial vibrissae in this species consist of a prominent tuft of long carpal hairs at the wrist.

Our only adult voucher (AMNH 266477), an old male, had external measurements of 286 × 345 × 63 × 31 mm and weighed 620 g. Selected craniodental measurements of this specimen fall within the known range of morphometric variation for the species (Marshall, 1978b): condylobasal length, 65.7 mm; length of molars, 14.5 mm; palatal breadth, 23.5 mm; palatal length, 42.7 mm; least interorbital breadth, 13.1 mm; least postorbital breadth, 8.4 mm; zygomatic breadth, 39.0 mm; length of nasals, 31.8 mm. Both of our other vouchers are juveniles.

REMARKS: *Lutra minima* Zimmermann (1780) was based on Buffon's (1776) description of the "petite loutre d'eau douce de Cayenne", so our specimens are practically topotypes. Krumbiegel (1940a) and Marshall (1978b) both recognized four subspecies, but the necessity for a trinomial nomenclature for water opossums has yet to be demonstrated by any substantive analysis of character data. In the event that any subspecific distinctions are warranted, the Paracou population would obviously be referable to the nominate form.

FIELD OBSERVATIONS: Water opossums were commonly seen in all of the four named stream systems that have their headwaters in our study area; even the smallest and shallowest creeks were frequented (fig. 9). Because this species has bright eyeshine, is boldly marked, and splashes noisily while swimming or wading, it is not difficult to observe despite its nocturnal habits. Nevertheless, the occurrence of *Chironectes* at Paracou was previously unsuspected by the forestry workers and local hunters whom we interviewed.

One of our three vouchers was taken in a large (ca. 25 × 30 × 81 cm) wire live trap set in a small (ca. 2 m wide) shallow (ca. 15

Fig. 9. Aquatic habitat of *Chironectes minimus* in primary forest at Paracou. Water opossums were encountered almost every night that we worked near such small streams, most of which were less than 2 m wide and 50 cm deep. Streams frequented by *C. minimus* at Paracou had clear tea-colored (black) water and flowed slowly over mostly sandy beds. Other nocturnal vertebrates encountered in the same streams included potential predators such as caimans (*Paleosuchus* sp.) and anacondas (*Eunectes murinus*).

cm deep) stream in primary forest; the trap was unbaited, but rows of stakes were driven unto the streambed on either side to funnel animals moving downstream into the trap opening. The other two vouchers were collected by shooting. In addition, we recorded 23 unvouchered observations of water opossums, of which 2 were based on juveniles trapped in small (145 × 145 × 410 mm) wire live traps set in streams, and 21 were sightings of free-ranging individuals.

All of our 26 (vouchered and unvouchered) records of water opossums at Paracou were of animals trapped or sighted while they waded or swam in primary forest streams at night. Most free-ranging individuals alarmed by our presence quickly swam away, but two animals left the water and disappeared in dense streamside vegetation, and another entered a burrow near the water's edge. With the exception of a pair of animals apparently engaged in an aggressive interaction, all of our sightings were of solitary individuals.

Didelphis marsupialis Linnaeus

VOUCHER MATERIAL: AMNH 266456–266460, 266462–266466, 266468, 266470, 266471, 266473, 266475, 267367; MNHN 1995.895–1995.901. Total = 23 specimens (not including pouch young).

IDENTIFICATION: All of our specimens of *Didelphis* from Paracou are referable to the large, black-eared species *D. marsupialis,* the type locality of which was restricted by Thomas (1911a) to Surinam. Our material agrees in all qualitative details with Husson's (1978) description of Surinamese topotypes, but three of the four adults measured by Husson are larger than any collected at Paracou. To evaluate possible size differences, we borrowed Surinamese material for side-by-side comparisons with our vouchers; however, only four skin-and-skull preparations of adult specimens (all females) could be located. No differences in external characters were observed between Surinamese and French Guianan exemplars, and the measurement data we obtained (table 2) do not suggest any appreciable morphometric divergence. Considerable ontogenetic size variation is apparently characteristic of *Didelphis* species (Allen, 1901, 1902; Gardner, 1973), and it seems likely that Husson's large specimens were just old animals that may have been preserved because of their unusual dimensions. The essential identity of the Surinamese and French Guianan material we examined supports the conclusions (hitherto undocumented by published comparisons) of Thomas (1888) and Allen (1902) that *D. karkinophaga* Zimmermann and *D. cancrivora* Gmelin (both based on "Le Crabier", an opossum described by Buffon from Cayenne) are junior synonyms of *D. marsupialis.*

Julien-Laferrière (1991) reported *Didelphis albiventris* and *D. marsupialis* as occurring syntopically in primary forest at Piste St.-Élie (only 14 km WNW of Paracou), the first published record of the former species from French Guiana. Catzeflis et al. (1997) subsequently reported both species from primary forest near Petit Saut (about 28 km SSW of Paracou). In view of these records of sympatry from nearby localities, our failure to record the presence of *D. albiventris* at Paracou merits comment.

The diagnostic morphological characters of *Didelphis marsupialis* and *D. albiventris* are sufficiently striking that collected specimens cannot be misidentified by competent researchers alert to the possible presence of both species. In the Guiana subregion of Amazonia, these taxa are readily distinguished by facial markings (bolder in *albiventris* than in *marsupialis*; Mondolfi and Pérez-Hernández, 1984), ear color (the pinnae are usually tipped with white in *albiventris* but are entirely black in adult *marsupialis*; op. cit.), caudal pelage (the furred basal portion of the tail is conspicuously longer in *albiventris* than in *marsupialis*; M. D. Engstrom, personal commun.), and size (*albiventris* is smaller; see measurements of the upper molar row of *albiventris* tabulated by Mondolfi and Pérez-Hernández, 1984). Correlated molecular characters that may be useful for discriminating *albiventris* and *marsupialis* were recently discussed by Lavergne et al. (1997).

Although *D. albiventris* is definitely absent from our voucher material, we did not collect every individual *Didelphis* that we encountered at Paracou. Because many animals were sighted in dense vegetation where

TABLE 2
Measurements (mm) and Weights (g) of Adult Specimens of *Didelphis marsupialis* from French Guiana and Surinam[a]

	Paracou vouchers		Surinamese females[d]
	Males[b]	Females[c]	
HBL	416 (405–437) 5	422 (405–446) 4	432 (397–500) 4
LT	437 (425–445) 5	430 (366–497) 4	407 (379–433) 4
HF	64 (61–66) 5	62 (56–66) 4	61 (56–63) 4
Ear	58 (53–61) 5	60 (55–63) 4	63 (62–63) 4
CBL	99.4 (96.3–103.5) 5	102.1 (96.9–105.7) 4	99.3 (97.3–101.1) 4
LM	20.8 (20.1–21.6) 5	20.3 (19.8–20.8) 2	19.7 (18.7–20.9) 4
PB	29.5 (28.8–30.1) 5	30.6 (29.9–31.2) 3	31.2 (28.9–33.3) 4
PL	60.9 (58.8–64.4) 5	63.2 (61.8–64.6) 3	61.0 (59.9–61.7) 4
LIB	19.0 (18.1–20.1) 5	19.8 (19.1–21.5) 4	19.9 (18.3–21.8) 4
ZB	50.7 (49.4–53.2) 5	51.0 (49.8–52.0) 3	52.3 (48.5–55.1) 4
Wt	1393 (1025–1700) 5	1298 (1190–1460) 4	1450 (1300–1500) 4

[a] Summary statistics include the sample mean, the observed range (in parentheses), and the sample size.
[b] AMNH 266457, 266459, 266468, 266471; MNHN 1995.900.
[c] AMNH 266465; MNHN 1995.896–1995.898.
[d] Topotypes; measured specimens were collected within 100 km of Paramaribo (CM 52697, 52702, 52716, 52724).

facial markings and other potentially informative details could not be distinguished, it is therefore possible that this species was seen but not recognized. Unfortunately, *Didelphis* virtually disappeared from our study area from 1992 to 1994, so we had little opportunity to collect specimens after we learned that *D. albiventris* could be expected to occur locally.

OTHER SPECIMENS EXAMINED: **Surinam**—*Brokopondo,* Brownsberg Nature Park (CM 52697); *Coronie,* Totness (CM 52702); *Saramacca,* Bigi Poika (CM 52716, 52724). Listed specimens are adult skin-and-skull preparations; other Surinamese material examined (CM, FMNH) are immature (subadults, juveniles) or incomplete (skull only/skin only) specimens that are not useful for taxonomic comparisons.

FIELD OBSERVATIONS: All of our unambiguous records of *Didelphis marsupialis* from Paracou are based on collected specimens. Of these, 15 (65%) were trapped and 8 (35%) were shot. Nine specimens (39%) were trapped or shot in trees or other elevated substrates at heights ranging from 0.3 to 15 m above the ground, whereas the remainder were trapped or shot on the ground. Of 21 specimens accompanied by habitat data, 11 (52%) were taken in clearings, roadside secondary growth, or other disturbed habitats; the other 10 (48%) were taken in primary forest, at both well-drained and swampy sites. All specimens were shot or trapped at night, and all unvouchered sightings of *Didelphis* were also nocturnal. All encountered individuals were solitary; no collected female was carrying suckling young.

Gracilinanus emiliae (Thomas)
Figures 11A, 11B, 12A, 17C, 17D, 18C, 18D

A single specimen from Paracou (AMNH 267006) is the first of this widespread but rarely collected species to be reported from French Guiana. Because the brief accounts by Thomas (1909), Tate (1933), Husson (1978), and Hershkovitz (1992) are inadequate for evaluating morphological similarities and differences with other congeners, we redescribe the species below.

TYPE MATERIAL: The holotype only, a male skin with skull and mandibles (BMNH 9.3.9.10) collected by Emilie Snethlage on 13 February 1909 at "Para" (= Belém, formerly known as Pará), Brazil. The type was described by Thomas (1909: 379) as a "subadult", by Tate (1933: 189) as a "young adult", and by Hershkovitz (1992: 33) as a "juvenal". The animal is, in fact, very nearly

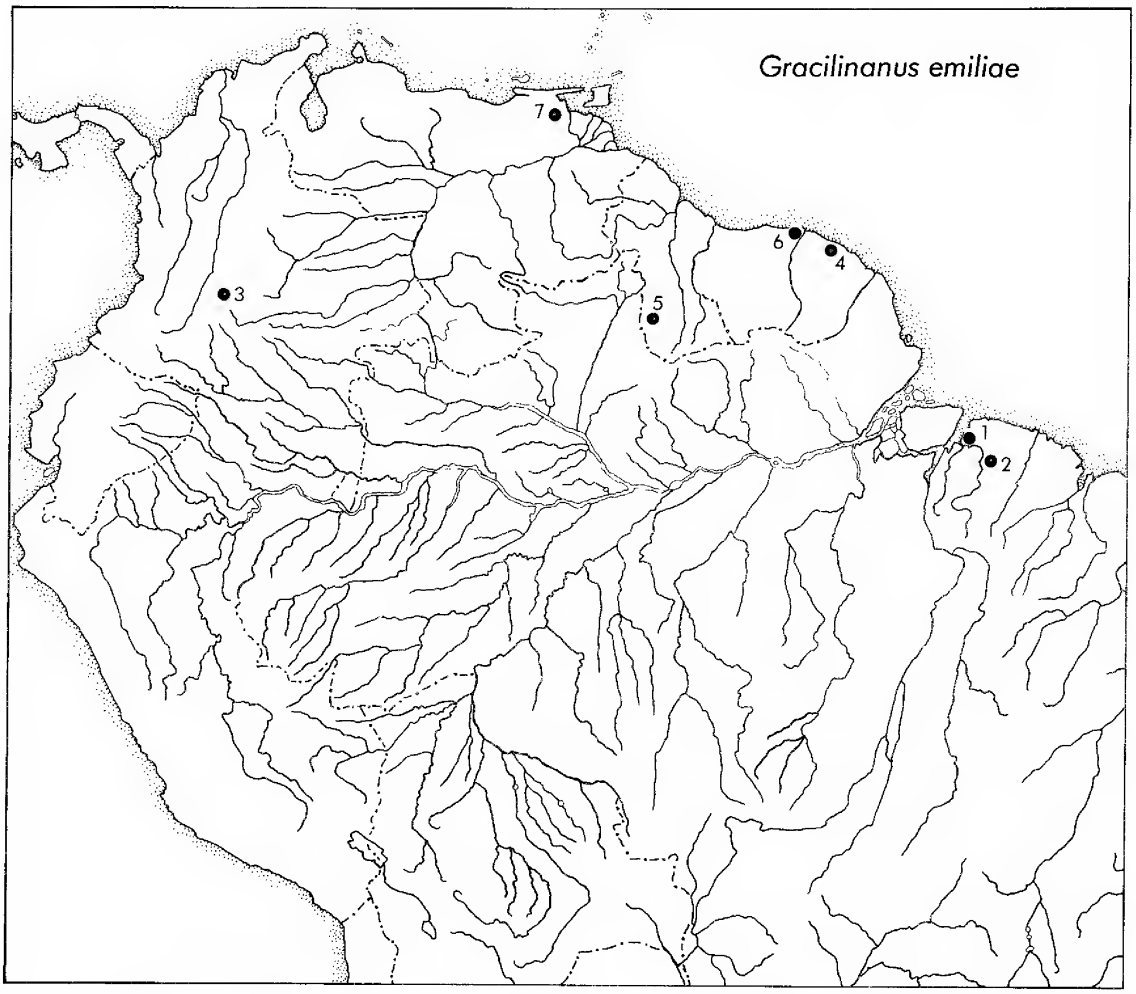

Fig. 10. Known collection localities for *Gracilinanus emiliae* based on specimens examined. **1,** BRAZIL, *Pará,* Belém; **2,** BRAZIL, *Pará,* Capim; **3,** COLOMBIA, *Meta,* Los Micos; **4,** FRENCH GUIANA, Paracou; **5,** GUYANA, *Upper Takutu-Upper Essequibo,* Dadanawa; **6,** SURINAM, *Marowijne,* Langamankondre; **7,** VENEZUELA, *Monagas,* 47 km SE Maturín.

adult with P3 and M4 both erupted but still a little below their adult positions in the toothrow.

Pine (1981: 59) suggested that the type locality should be construed as the state of Pará rather than the formerly eponymous city, but Thomas (always scrupulous about type localities) would surely have noted the lack of definite geographic information if he meant "Para" in the sense of a district larger than most European countries. A specimen collected at Capim (ca. 90 km ESE of Belém) provides independent evidence that the species may occur in the environs of the city.

DISTRIBUTION: Specimens that we examined document the presence of *Gracilinanus emiliae* in eastern Colombia, eastern Venezuela, southern Guyana, northern Surinam, northern French Guiana, and eastern Brazil (fig. 10). Several other published localities for this species are erroneous or unreliable (see Remarks, below).

EMENDED DESCRIPTION: Very small murine opossums (table 3) with smooth (not woolly) adult pelage; unruffled dorsal fur dull reddish brown, but basal two-thirds dark gray; ventral fur pure white or cream from chin to groin (the hairs self-colored, not grayish ba-

sally). Face marked by mask of black fur extending from mystacial pad to just behind outer canthus of eye on each side, and by narrow midrostral streak of pure orange fur; cheeks (below mask) white or cream-colored like throat; facial vibrissae (including long superciliary, mystacial, and genal hairs) mostly black (but some of the ventralmost genals are usually white); vibrissae of chin and throat (submental and interramal hairs) white. Ears not very large (just covering eye when laid forward over face), apparently naked (a sparse pelage of very short hairs is only visible under magnification), and very thin; opaque and pale basally (possibly yellow in life, but whitish in fresh alcoholic specimens); translucent and darker (brownish or grayish) distally. Gular glands (indicated by a naked or sparsely haired median patch of skin on the throat) present in all specimens examined, including one juvenile.

Wrists, ankles, and dorsal surface of feet covered with short pale (whitish or orange-tinted) hairs. Manus and pes each with six plantar pads (thenar, hypothenar, and four interdigitals); thenar and first interdigital pads of manus separated by at least two rows of minute epidermal tubercles; thenar and first interdigital pads fused on pes of one fluid specimen (AMNH 267006), touching but not fused on pes of two others (ROM 35465, 35466); central palmar surface of manus smooth (not densely tubercular); claws of manual digits II–V small, not extending beyond fleshy apical pads. Scrotal epidermis of holotype entirely unpigmented, of another subadult (AMNH 267006) with dark dorsal blotch surrounding suspensory stalk, of one fully adult specimen (ROM 35466) entirely dark. At least nine (4–1–4) abdominal-inguinal mammae present in one adult female (ROM 35465).

Tail much longer than head-and-body (table 3); less than 1 cm furry at base; uniformly dark (grayish or brownish) without pale blotches, bands, or countershading. Caudal epidermis covered with very small scales in annular or spiral series,[3] numbering 40–50 rows/cm at middle of tail (counts from three fluid specimens and two dried skins). Median hair of triplet emerging from posterior margin of each scale about two scale rows long, thicker than lateral hairs, but not grossly flattened or petiolate.

Skull (figs. 11, 12) with slender rostrum, incipiently beaded supraorbital margins, and absence of postorbital processes of frontals; orbits not conspicuously enlarged (delimited posteriorly by well-developed postorbital processes of jugals); braincase not greatly inflated, smooth and unmarked by prominent temporalis scars. Premaxillaries with small

TABLE 3
Measurements (mm) and Weights (g) of Subadult and Adult Specimens of *Gracilinanus emiliae*

	Brazil		Guianas		Colombia
	BMNH 9.3.9.10[a]	AMNH 203363	AMNH 267006	ROM 35465	FMNH 87924[b]
Age	subadult	adult	subadult	adult	adult
Sex	male	male	male	female	male
HBL	75	80	75	83	87
LT	142	150	138	142	143
HF	13	14	13[c]	14	16
Ear	16	15	17	17	16
CBL	22.0	23.7	21.3	23.8	23.8
LM	4.9[d]	5.0	4.9[d]	5.1	5.0
M1–M3[e]	4.2	4.4	4.1	4.4	4.4
PB	7.0	—	—	7.5	7.7
PL	11.9	12.9	11.7	12.8	12.9
LIB	4.2[f]	—	3.9	4.2	4.2
ZB	12.8	—	12.7	14.0	13.4[g]
Wt	—	10	10	—	—

[a] Type of *Marmosa emiliae* Thomas.

[b] Type of *Gracilinanus longicaudus* Hershkovitz.

[c] Remeasured from fluid specimen.

[d] Estimated value.

[e] Crown length of the first three upper molars.

[f] Tate's (1933: table 1) value of 5.3 mm for the interorbital breadth of this specimen (repeated in Hershkovitz, 1992: table 5) was obviously erroneous.

[g] Value from Hershkovitz (1992: table 5). The right zygomatic arch of this specimen is now broken.

[3] The difference between spiral and annular arrangements of caudal scales cited by Tate (1933) as a useful character for diagnosing species groups of *Marmosa* (sensu lato) is less than obvious within *Gracilinanus* (part of Tate's *microtarsus* group). As noted by Hershkovitz (1992), spiral or annular series may occur on the same tail, and the perceived arrangement may be subject to observer bias. With the examples at hand of *G. emiliae* it is difficult to determine which, if either, descriptor is appropriate.

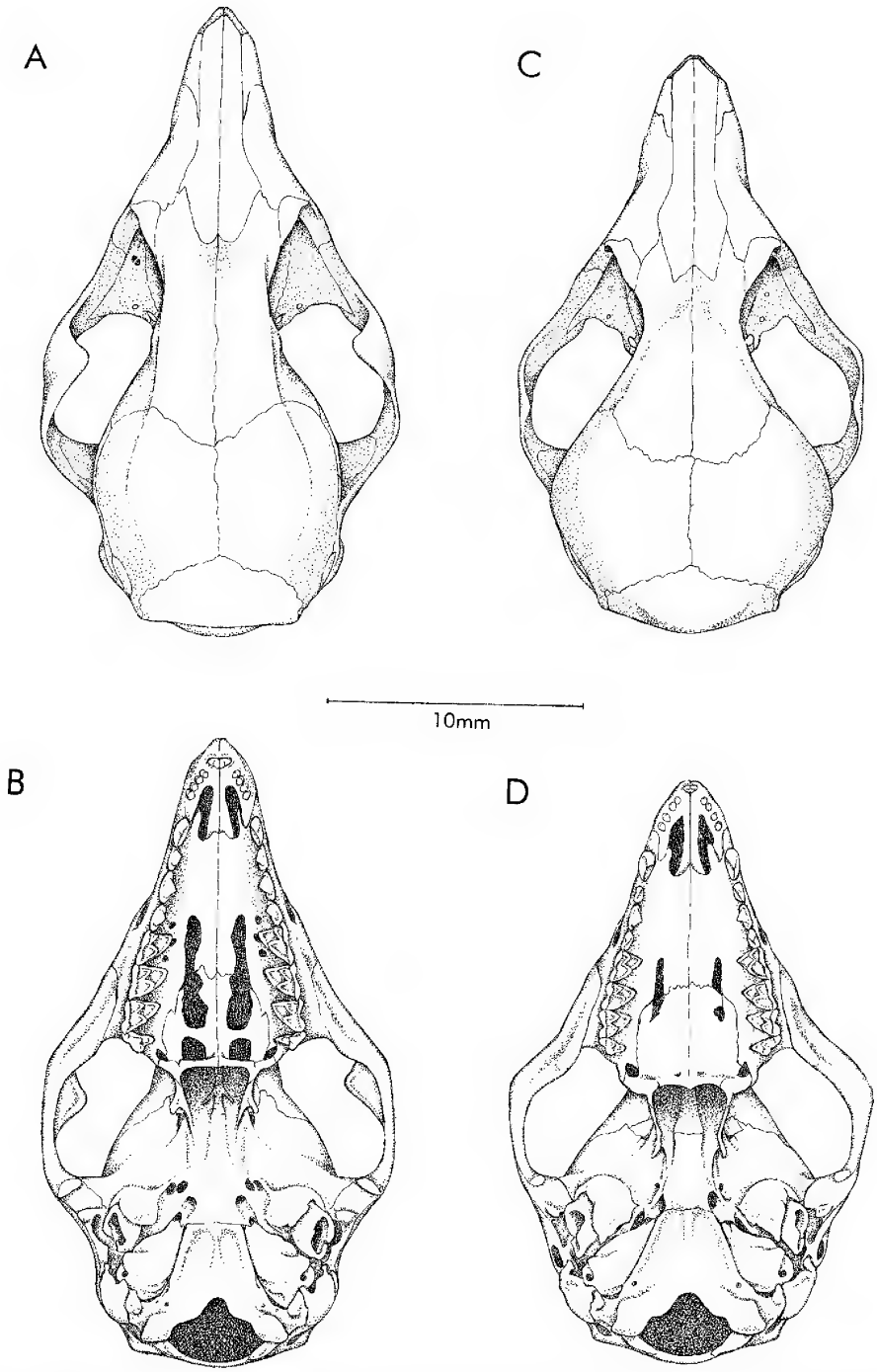

Fig. 11. Dorsal and ventral cranial views of (**A, B**) *Gracilinanus emiliae* (composite of AMNH 203363, AMNH 267006, and ROM 35466) and of (**C, D**) *Hyladelphys kalinowskii* (AMNH 267338). Differences in rostral length, interorbital morphology, size of the orbits, braincase shape, and palatal fenestration are among the taxonomic differences illustrated by these views.

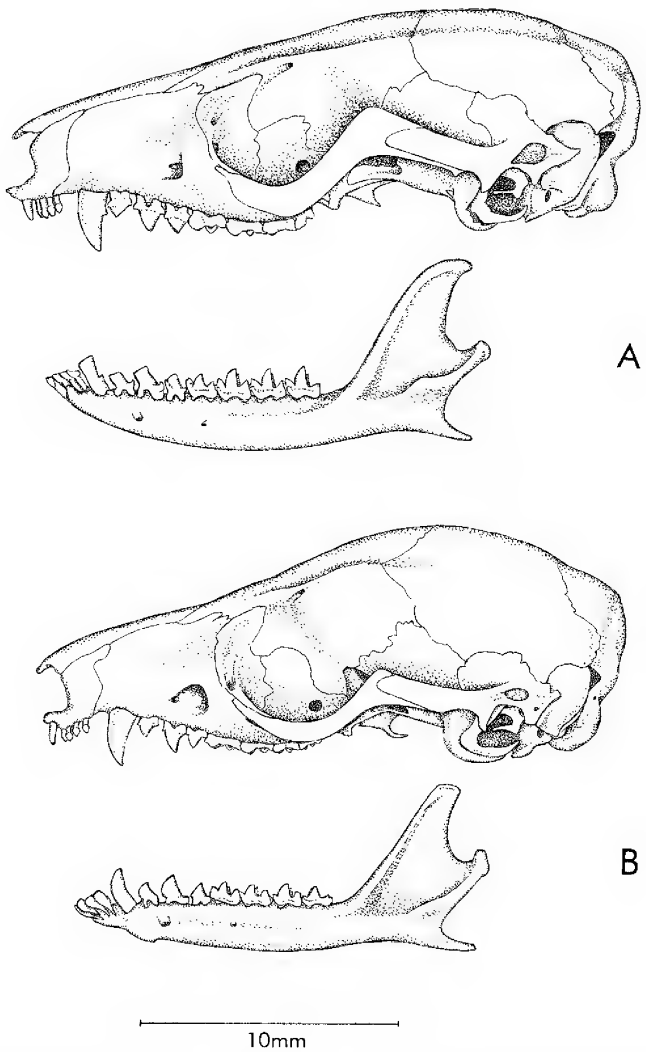

Fig. 12. Lateral views of crania and mandibles of (**A**) *Gracilinanus emiliae* and (**B**) *Hyladelphys kalinowskii* based on the same specimens as in figure 11. Prominent taxonomic differences illustrated in these views include orbital size, development of the postorbital process of the jugal, braincase shape, presence of accessory cusps on upper and lower canines, and relative reduction of the third premolar.

but distinct rostral process anterior to incisors; maxillary-premaxillary suture extending to posteriormost incisor alveolus; palate highly fenestrated, with large maxillopalatine and posteromedial (palatine) vacuities; one or more small maxillary palatal vacuities present unilaterally in one specimen (AMNH 203363), bilaterally in three others (BMNH 9.3.9.10, ROM 35466, RMNH 18231). Alisphenoid wing of auditory bulla with well-developed anteromedial process bridging foramen ovale.

Upper incisors 2–5 subequal (not increasing in size from front to back); upper canine with small posterior accessory cusp; lower canine procumbent and premolariform (with flattened blade-like apex and small posterior accessory cusp); deciduous third premolars (dP3/dp3) large and molariform (figs. 17, 18); permanent third upper and lower premolars (P3/p3) slightly smaller than second premolars (P2/p2); metacones much larger than paracones on M1–3.

COMPARISONS: *Gracilinanus emiliae* and a

sympatric taxon originally described by Hershkovitz (1992) as *G. kalinowskii* are similar in size and coloration (both have reddish-brown dorsal fur and pure white or cream-colored ventral fur), but they differ in many other characters as explained in the following account. *Marmosa lepida* (not known to occur at Paracou but reported from other localities in French Guiana and Surinam; appendix 1) is also externally similar to *G. emiliae.* Although adults of *M. lepida* are much larger than *G. emiliae,* immature specimens of the former species might be almost impossible to distinguish from the latter in the field. Cranially, adult *M. lepida* (see Husson, 1978: pl. 11) can be identified by their (1) distinctively longer premaxillary rostral processes, (2) prominent postorbital frontal processes, (3) lack of posteromedial palatal vacuities, (4) lack of anteromedial bullar processes, and (5) lack of mastoid exposure between the squamosal and parietal bones. Skulls of juvenile *M. lepida* that lack postorbital frontal processes can still be distinguished from *G. emiliae* by rostral, palatal, and bullar morphology, and by tooth size (see under Remarks, below).

REMARKS: Originally described as *Marmosa emiliae* (Thomas, 1909), this species was subsequently referred to *Didelphis* (subgenus *Grymaeomys*) by Matschie (1916), and to *Marmosa* (subgenus *Thylamys*) by Cabrera (1958). The current allocation of *emiliae* to *Gracilinanus* follows Gardner and Creighton (1989).

Gracilinanus longicaudus, named by Hershkovitz (1992) from a single specimen (FMNH 87924) collected in eastern Colombia, does not differ significantly from *G. emiliae* in any external, cranial, or dental character. According to the original description, "... the combination of small size, long tail, whitish underparts, incomplete eye ring, and narrow skull separates [*longicaudus*] from all other described species [of *Gracilinanus*]" (op. cit.: 39). However, the black mask of FMNH 87924 does, in fact, completely encircle the eye (a narrow border of black hairs is continuous below the lower lid and around the posterior canthus), and the other characters cited as diagnostic for *longicaudus* are matched by the type (and other referred specimens) of *emiliae.* Our side-by-side comparisons of AMNH 203363 (an adult male skin and skull from Capim, Brazil) with the holotype of *emiliae* in London and, later, with the holotype of *longicaudus* in Chicago, revealed no differences beyond those that might be expected among individuals from a single local population (for measurements, see table 3). We therefore regard *G. longicaudus* as a junior synonym of *G. emiliae.*

Eisenberg (1989) suggested that *Gracilinanus emiliae* might be conspecific with *G. microtarsus* from the Atlantic coastal rainforest of southeastern Brazil, but it would be difficult to select two more dissimilar congeners for comparison. Among other differences, *Gracilinanus microtarsus* is much larger and has a proportionately much shorter tail (see measurements in Tate, 1933; Hershkovitz, 1992), the ventral fur is buffy and gray-based, the supraorbital margins are not beaded, and the crowns of I2–5 increase in size from front to back.

Gardner and Creighton (1989), Hershkovitz (1992), and Gardner (1993) listed *Marmosa agricolai* Moojen (1943) as a synonym of *Gracilinanus emiliae,* but Moojen's illustration (op. cit.: fig. 1) and description are difficult to reconcile with this decision: the ratio of tail to head-and-body for *agricolai* is only 1.28, the maxillary-premaxillary suture (as drawn) does not extend anteriorly to I5, the frontals are shown without supraorbital beads, the zygomatic arches are widely flared, the illustrated bullae appear to lack anteromedial processes, the upper canine appears to have a small anterior accessory cusp, and the third upper premolar (as drawn) is larger than the second. The type of *agricolai* (in Rio de Janeiro) should be reexamined to evaluate the true status and relationships of this nominal species.

We examined the two Brazilian specimens identified by Patterson (1992) as *Gracilinanus emiliae* and found them to be immature examples of *Marmosa lepida.* Both skulls have very long rostral processes of the premaxillae, lack posteromedial palatal vacuities, and their rounded alisphenoid bullae lack anteromedial processes; the erupted elements of the molar dentition are also larger than those of any specimens of *G. emiliae* but match the homologous teeth of adult *M. lepida* from eastern Peru (e.g., AMNH

78001, 98656). Because immature *Marmosa lepida* can be confused with *Gracilinanus emiliae* in size and external appearance, literature records of the latter (e.g., Ávila-Pires, 1964) should be regarded as suspect until diagnostic characters can be reconfirmed from specimens.

OTHER SPECIMENS EXAMINED: **Brazil**—*Pará,* Belém (BMNH 9.3.9.10, type), Capim (AMNH 203363). **Colombia**—*Meta,* Los Micos (FMNH 87924, type of *Gracilinanus longicaudus*). **Guyana**—*Upper Takutu-Upper Essequibo,* 12 km E Dadanawa (ROM 35465, 35466), no other locality data (ROM 33807). **Surinam**—*Marowijne,* Langamankondre (RMNH 18231). **Venezuela**—*Monagas,* 47 km SE Maturín (USNM 385066).

FIELD OBSERVATIONS: Our single specimen from Paracou was shot at 22:18 hours on 21 October 1992 as it perched about 4 m above the ground in dense secondary growth along a dirt road through well-drained forest (fig. 13).

Hyladelphys, new genus

DIAGNOSIS: Very small didelphids distinguished from all other family members by the following combination of traits: four mammae in two abdominal-inguinal pairs; dorsolateral margins of frontals beaded and strongly convergent anteriorly, without postorbital processes; premaxillae short, without rostral process anterior to incisor row; posteromedial (palatine) palatal vacuities absent; tympanic wing of alisphenoid without a well-developed anteromedial strut forming secondary foramen ovale; I2–5 not increasing in size from front to back, their crowns asymmetrical and nonoverlapping; upper canine without anterior or posterior accessory cusps; P2 much larger than P3; deciduous premolars (dP3/dp3) very small and nonmolariform; molars not highly carnassialized (paracone smaller than metacone on M1–2, but paracone and metacone subequal on M3); lower canine not premolariform.

TYPE SPECIES: *Gracilinanus kalinowskii* Hershkovitz, 1992.

CONTENT: *Hyladelphys* currently contains only the type species.

ETYMOLOGY: From ὑλη (wood or forest), sometimes used in its Latinized form (hylaea) in reference to the predominant vegetation of the Amazonian lowlands (e.g., by Ducke and Black, 1953); and δελφύς (womb), a traditional suffix for New World marsupial genera.

Hyladelphys kalinowskii (Hershkovitz)

Figures 11C, 11D, 12B, 15A, 16A, 17A, 17B, 18A, 18B, 19B

Three specimens from Paracou (AMNH 267338, 267339; MNHN 1995.903) and one from Guyana (kindly loaned to us for identification by M. D. Engstrom) represent extraordinary range extensions of this distinctive species, originally described as *Gracilinanus kalinowskii* by Hershkovitz (1992) on the basis of two Peruvian specimens. We provide an emended description with comparisons and remarks based on this new material and our reexamination of Hershkovitz's type series.

TYPE MATERIAL: The holotype, an adult female skin and skull (FMNH 89991), collected on 9 July 1958 by Celestino Kalinowski at Hacienda Cadena (890 m elevation), Marcapata, Departamento Cuzco, Peru; and the paratype, also an adult female skin and skull (FMNH 65754), collected in October 1948 by J. M. Schunke at Chanchamayo (1100 m elevation), Departamento Junín, Peru.

DISTRIBUTION: Known only from Amazonian Peru, southern Guyana, and northern French Guiana (fig. 14).

EMENDED DESCRIPTION: Very small in all external and craniodental dimensions (table 4). Body pelage smooth (not woolly); dorsal fur unpatterned dull reddish brown, but basal two-thirds of hairs dark gray; ventral fur pure white or cream from chin to groin (the hairs self-colored, not grayish basally). Face boldly marked by broad mask of black fur extending from mystacial pad to base of ear on each side, and by prominent median streak of very pale orange fur extending from between eyes to rhinarium; cheeks (below mask) white like throat. Facial vibrissae (including long superciliary, mystacial, and genal hairs) mostly black (but a few of the ventralmost genals are white); vibrissae of chin and throat (submental and interramal hairs) white. Ears very large (covering eyes and extending to mystacial pads when laid forward

Fig. 13. Secondary growth bordering a narrow dirt road through our study area at Paracou. Our only specimen of *Gracilinanus emiliae* was taken in this habitat, but primary forest occurs only a few meters away and it is not known which successional stage is typical of this rarely collected species. More commonly encountered inhabitants of secondary growth at Paracou include *Didelphis marsupialis, Marmosa murina, Micoureus demerarae, Philander opossum, Dasypus novemcinctus, Saguinas midas, Potos flavus, Neacomys paracou, Oligoryzomys fulvescens, Oryzomys megacephalus,* and *Proechimys cuvieri.*

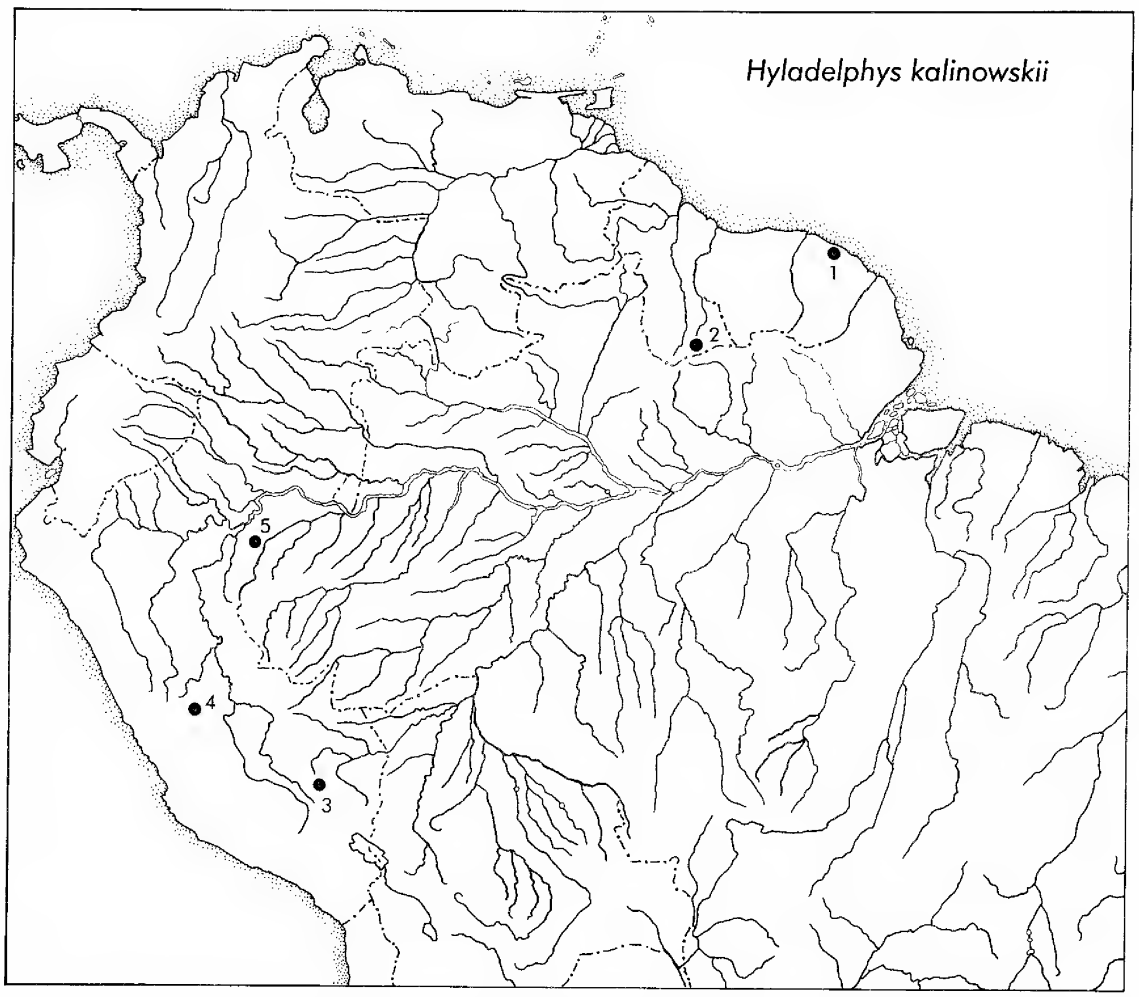

Fig. 14. Known collection localities of *Hyladelphys kalinowskii* based on specimens examined. **1,** FRENCH GUIANA, Paracou; **2,** Guyana, *East Berbice-Corentyne,* New River Falls; **3,** PERU, *Cuzco,* Hacienda Cadena; **4,** PERU, *Junín,* Chanchamayo; **5,** PERU, *Loreto,* Nuevo San Juan on Río Gálvez.

over face), apparently naked (a sparse pelage of tiny hairs is visible only under magnification), and paper-thin; opaque and bright yellow-orange basally in fresh specimens (this color fading to white after a few months in alcohol), translucent and brownish distally. Eyes very large. Throat glands apparently absent.[4]

Wrists, ankles, and dorsal surface of metapodials covered with short, orange fur; manus and pes each with six plantar pads (thenar, hypothenar, and four interdigitals), the thenar and first interdigital touching but not fused on either manus or pes; central palmar surface smooth (not densely tubercular); claws of manual digits II–V large, extending beyond fleshy apical pads. Scrotum (of one adult male, AMNH 267338) pigmented,

[4] Throat glands in murine opossums are indicated by a midventral gular patch of pigmented hair or bare skin (Tate, 1933). Although Hershkovitz (1992: 11) remarked that "neither marker is present in the two females of *G. kalinowskii*", the paratype (FMNH 65754) was subsequently described as resembling the holotype externally "but with gular gland evident" (op. cit.: 38). We carefully examined the throat of FMNH 65754 under a dissecting microscope and found no external trace of glandular development. No discolored fur or bare patches are present on the throats of any of the four fluid specimens we examined from the Guianas.

TABLE 4
Measurements (mm) and Weights (g) of Adult Specimens of *Hyladelphys kalinowskii*

	Peru		Guyana	French Guiana		
	FMNH 89991[a]	FMNH 65754[b]	ROM 34271	MNHN 1995.903	AMNH 267338	AMNH 267339
Sex	female	female	female	female	male	female
HBL	89	91	85	78	76	77
LT	117	110	102	113	112	107
HF	16	15	13[c]	15	15	14[c]
Ear	18	15	19	18	19	19
CBL	23.6	23.7	21.8	21.4	21.4	21.2
LM	4.6	4.6	4.4	4.3	4.3	4.2
PB	7.3	7.4	6.9	6.6	7.0	6.6
PL	12.5	—	11.8	11.5	11.9	11.5
LIB	3.7	3.9	3.8	4.0	3.9	3.9
ZB	15.0	—	13.9	—	13.8	13.7
Wt	—	—	—	13	18	18

[a] Holotype.
[b] Paratype.
[c] Remeasured from fluid specimen.

blue. Mammae 2–0–2 = 4, in two abdominal-inguinal pairs (without an unpaired median teat; fig. 15).[5]

Tail not very long and without furry base; dark (brownish) above and below, but indistinctly banded by absence of pigment over vertebral articulations. Caudal epidermis scaly beneath sparse covering of fine hairs; caudal scales in annular or spiral series, numbering about 25–35 rows/cm at middle of tail (counts from four fluid specimens). Median hair of triplet emerging from posterior margin of each scale usually about three scale rows long, thicker than lateral hairs but not grossly flattened or petiolate.

Skull (figs. 11, 12) with distinctively short, blunt rostrum; beaded and anteriorly convergent supraorbital margins; no postorbital frontal processes; very large orbits (their posterior limits indicated by weakly developed postorbital processes of the jugals); and laterally inflated braincase. Premaxillae without rostral process anterior to incisors; maxillary-premaxillary suture not extending to posteriormost incisor alveolus; maxillopalatine vacuities narrow, discontinuous in some specimens; posteromedial (palatine) and maxillary vacuities absent.[6] Alisphenoid wing of auditory bulla without a well-developed anteromedial process bridging the foramen ovale (see Remarks, below).

Upper incisors 2–5 subequal (not increasing in size from front to back), asymmetrical (the crowns with anterior but no posterior styles), and nonoverlapping (fig. 16); upper and lower canines without accessory cusps; lower canine erect and not premolariform; deciduous third premolars (dP3/dp3) extremely reduced, not molariform (figs. 17, 18); permanent upper and lower third pre-

[5] Hershkovitz (1992: 37) gave the mammary formula of *kalinowskii* as 7–1–7 = 15. This notation corresponds to what he described earlier (op. cit.: 11) as the "... *prime* formula for *Gracilinanus* ... of which the pectoral is 2–0–2 = 4, the abdominal-inguinal, 5–1–5 = 11. The *functional* teat formula may be the same or less, depending on the number of attached young. Unused nipples are more-or-less resorbed" (italics original). Contrary to this last assertion, however, unused teats remain everted and are not "resorbed" in adult female marsupials (Bresslau, 1920; Tyndale-Biscoe and Renfree, 1987). Although unused teats are smaller than actively lactating teats, accurate mammary counts can be obtained even from anestrous adults. All of the five adult females of *Hyladelphys kalinowskii* that we examined have four well-developed mammae in two abdominal-inguinal pairs; no other mammary loci were apparent, even with careful searching under high magnification.

[6] Hershkovitz (1992: 37–38) described the posteromedial vacuities of *Hyladelphys kalinowskii* as "small", but these fenestrae are absent in the holotype and the posterior palate of the paratype is destroyed. None of the specimens from Guyana and French Guiana have posteromedial vacuities.

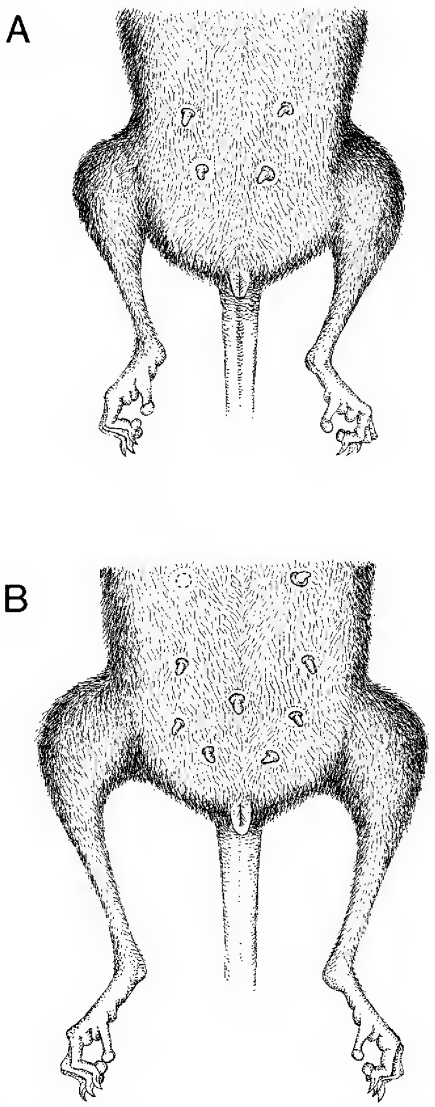

Fig. 15. Mammary morphology of adult female specimens of *Hyladelphys kalinowskii* (**A,** AMNH 267339) and *Marmosops parvidens* (**B,** AMNH 267344). Only two pairs of inguinal-abdominal teats are present in *H. kalinowskii,* whose mammary formula can be written as 2–0–2 = 4. By contrast, this specimen of *M. parvidens* has four pairs of inguinal-abdominal teats plus an unpaired median teat (4–1–4 = 9).

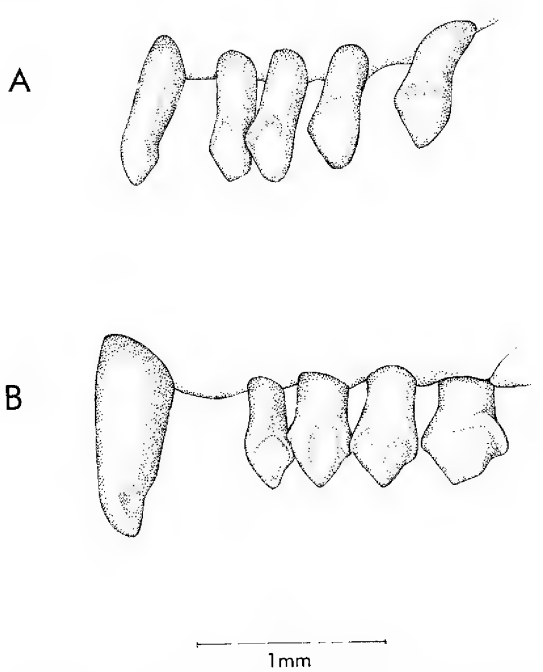

Fig. 16. Details of upper incisor morphology of (**A**) *Hyladelphys kalinowskii* (AMNH 267338) and (**B**) *Marmosops pinheiroi* (AMNH 267341). In all examined specimens of *Hyladelphys,* the crowns of I2–5 are narrow, asymmetrical, and widely spaced, with no consistent size increase from front to back. By contrast, the crowns of I2–5 in *Marmosops* are broad, symmetrical, overlapping or closely approximated rhomboids of posteriorly increasing size.

molars (P3/p3) much smaller than second premolars (P2/p2); molars not highly carnassialized (metacone larger than paracone on M1 and M2, but metacone and paracone subequal on M3).

VARIATION: The four fluid-preserved specimens (with extracted skulls) from Guyana and French Guiana agree in all qualitative characters with the Peruvian holotype despite several inconsistencies between Hershkovitz's (1992) original description and that given above (see footnotes 4–6). The Peruvian specimens are slightly larger than French Guianan material (table 4), but the apparent size difference (perhaps best indexed by molar measurements) is no more than might be expected of conspecific samples collected almost 3000 km apart. The alisphenoid bullae of the holotype and of all four specimens from the Guianas lack anteromedial processes, but weakly developed processes (which are not fused to the floor of the braincase as they normally are in *Gracilinanus, Marmosops,* and *Thylamys*) are present on the anteromedial aspect of both alisphenoid bullae of the paratype. We interpret this as intraspe-

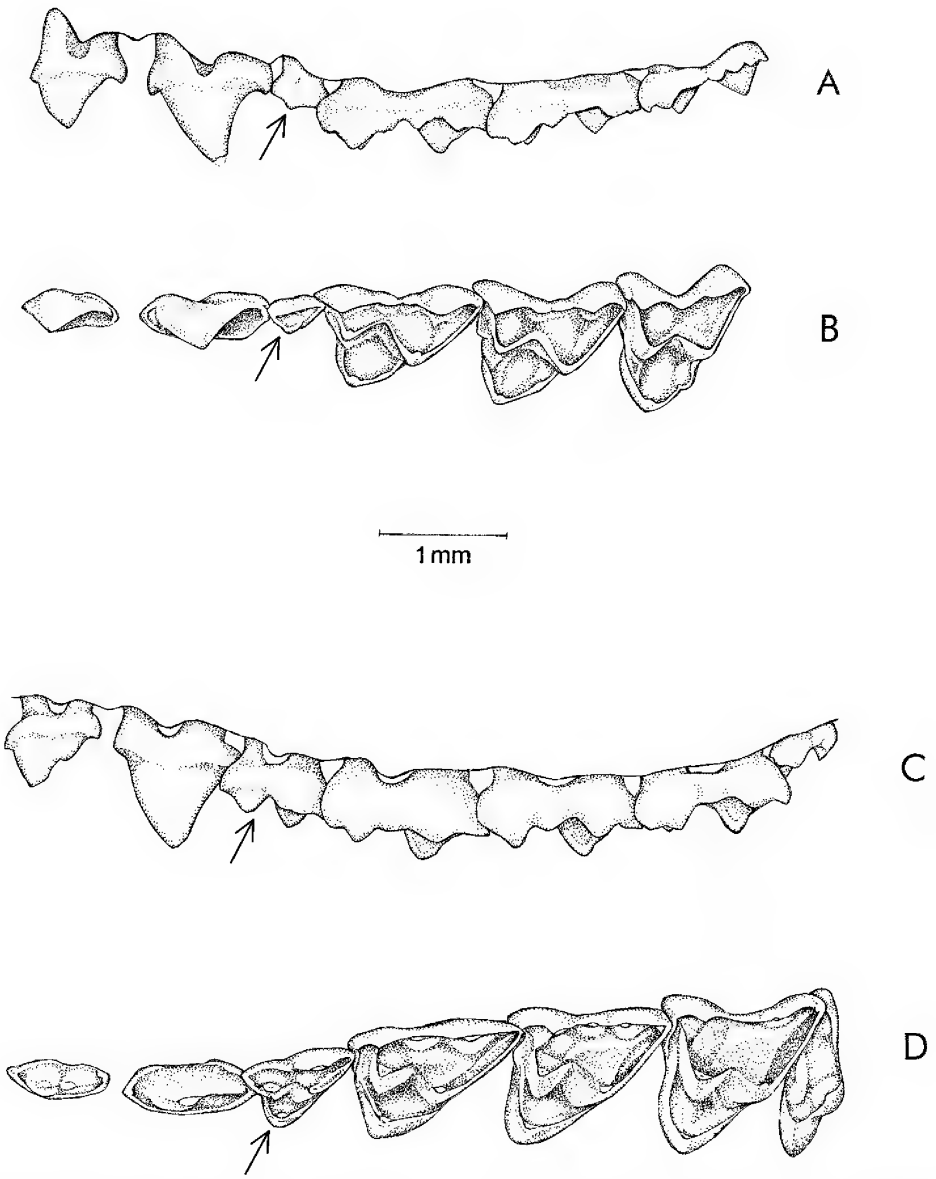

Fig. 17. Lateral and occlusal views of the left upper postcanine dentition of juvenile *Hyladelphys kalinowskii* (**A, B,** MUSM 11031) and *Gracilinanus emiliae* (**C, D,** USNM 385066) showing taxonomic differences in size and shape of the deciduous third premolar (dP3, arrows; see text). The fourth upper molar is unerupted in this example of *H. kalinoswkii* and incompletely erupted in *G. emiliae.*

cific variation because the paratype is not morphologically remarkable in any other respect.

COMPARISONS: *Hyladelphys kalinowskii* appears to differ from all other Recent didelphids in at least two qualitative characters. As far as is known, well-preserved adult females of other didelphid taxa uniformly exhibit odd-numbered mammary counts due to the presence of an unpaired median teat (fig. 15B); by contrast, caenolestids, microbiotheriids, and Old World marsupials have even-numbered mammary counts because their teats are bilaterally paired (Bresslau, 1920; Osgood, 1921, 1943; Tate, 1933, 1947, 1948). All reports of even-numbered didel-

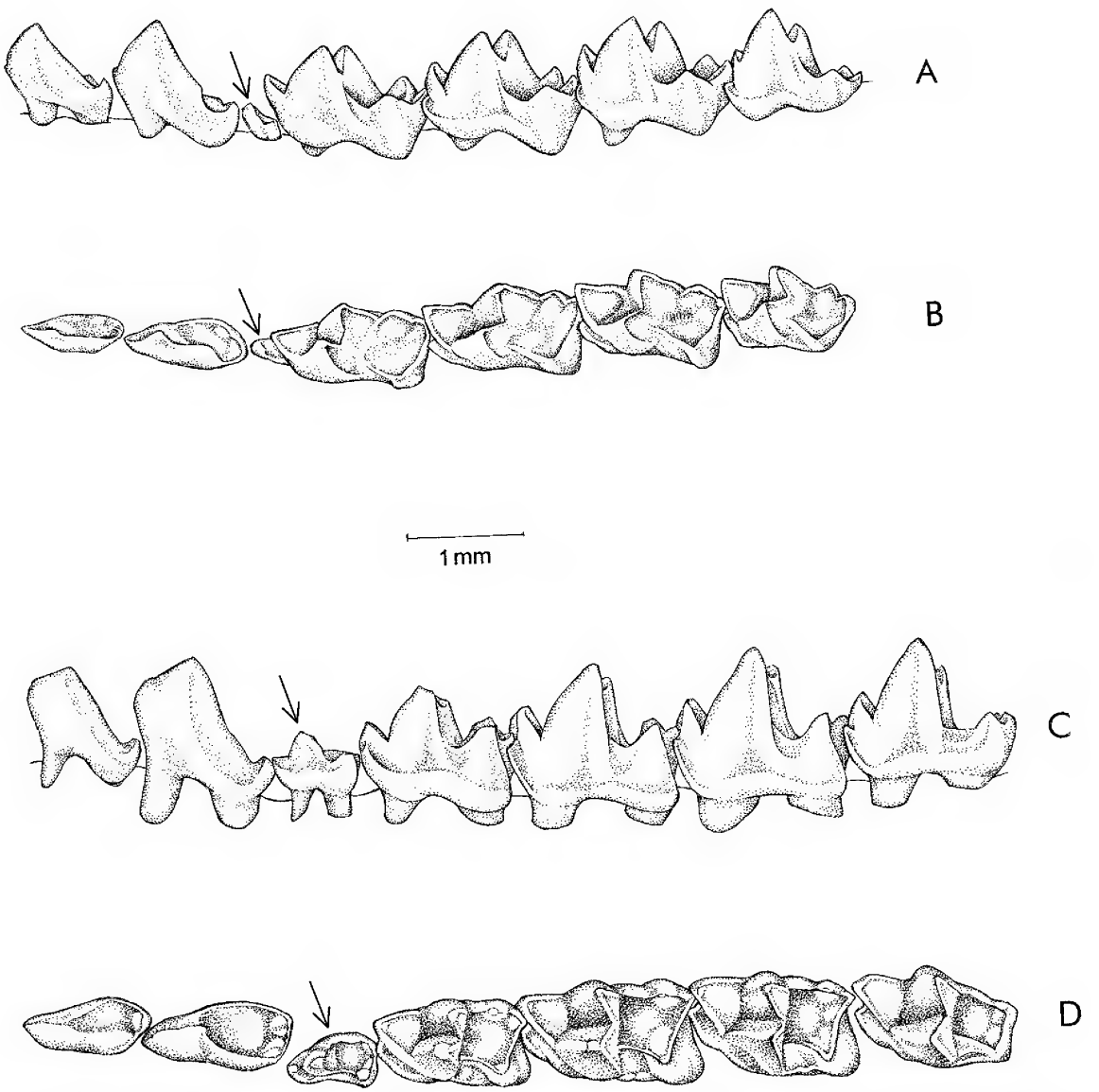

Fig. 18. Lateral and occlusal views of the left lower postcanine dentitions of juvenile *Hyladelphys kalinowskii* (**A, B,** MUSM 11031) and *Gracilinanus emiliae* (**C, D,** USNM 385066) showing taxonomic differences in the size and shape of the deciduous third premolar (dp3, arrows; see text).

phid mammary counts that we investigated were either field observations of lactating teats only (e.g., Hershkovitz, 1997: table 4), or were observations from specimens with midventral incisions that might have destroyed the median nipple (e.g., Marshall's [1978a] count of four mammae from an FMNH skin of *Glironia venusta*; W. T. Stanley, personal commun.). By contrast, our observations of identical (2–0–2 = 4) mammary configurations in two *Hyladelphys* skins from Peru and two fluid-preserved specimens from French Guiana suggest that these are not rare variants or preservational artifacts. Instead, this taxon appears to be genuinely divergent from other didelphids in a character that displays considerable higher-taxonomic stability among marsupials.

Hyladelphys also differs markedly from other didelphids in the morphology of its de-

TABLE 5
Morphology and Size of Milk Premolars among Didelphids and Other Marsupials

	dP3		dp3		
	Morphology[a]	Size (%)[b]	Morphology[c]	Size (%)[b]	Exemplar
Didelphidae					
Caluromys derbianus	M	55	I	45	AMNH 139281
Chironectes minimus	M	96	M	82	AMNH 266478
Didelphis marsupialis	M	79	M	73	AMNH 266456
Gracilinanus agilis	M	42	I	38	AMNH 133224
Hyladelphys kalinowskii	N	8	N	5	MUSM 11031
Lutreolina crassicaudata	M	65	M	72	AMNH 210424
Marmosa murina	M	55	I	42	AMNH 266417
Marmosops noctivagus	M	43	M	48	AMNH 272715
Metachirus nudicaudatus	M	61	M	62	AMNH 267364
Micoureus demerarae	M	40	I	38	AMNH 266434
Monodelphis brevicaudata	M	43	M	43	AMNH 16953
Philander opossum	M	67	M	79	AMNH 266997
Thylamys pusillus	M	44	M	36	AMNH 246252
Dasyuridae					
Antechinus swainsonii	N	18	N	17	AMNH 65719
Murexia longicaudata	N	11	N	8	AMNH 101970
Myoictis melas	N	2	N	1	AMNH 152009

[a] Molariform upper premolars (M) are unambiguously tribosphenic, with distinct protocone, paracone, and metacone. Nonmolariform upper premolars (N) do not have cusps that can be clearly homologized with those of tribosphenic teeth.

[b] Occlusal area expressed as a percentage of the occlusal area of the adjacent first molar (M1 or m1). We estimated the occlusal area of approximately triangular teeth as $\frac{1}{2}$ length × width, of roughly oblong teeth as length × width, and of peg-like teeth (with approximately round occlusal outlines) as $\pi(\frac{1}{2}\text{ width})^2$.

[c] Molariform lower premolars (M) are unambiguously tribosphenic, with distinct talonids and complete trigonids. Nonmolariform upper premolars (N) do not have distinct talonids and trigonids. An intermediate condition (I) is represented by teeth with distinct talonids but incomplete trigonids.

ciduous dentition. Whereas previous descriptions of didelphid milk premolars have consistently reported these teeth as large and molariform (Flower, 1867; Thomas, 1888; Bensley, 1903; Tate, 1948; Archer, 1976b), there is in fact some substantial variation in the size and morphology of dP3/dp3 within the family (table 5). However, *Hyladelphys* is a conspicuous outlier: its milk teeth are much smaller than those of other confamilials, and they are uniquely nonmolariform in occlusal structure (figs. 17, 18). Instead, dP3/dp3 in *Hyladelphys* fall well within the range of milk-premolar morphologies seen in some Old World marsupial groups (Tate, 1947, 1948; Archer, 1976b; see illustrations in Luckett, 1993, 1994).

From superficially similar "marmosines", *Hyladelphys* differs in additional characters. Species of *Gracilinanus,* among which *H. kalinowskii* was previously classified, differ by having much smaller caudal scales (> 40 rows/cm), longer and narrower rostrums, less pronounced interorbital constrictions, smaller orbits, less inflated braincases, much more highly fenestrated palates, secondary foramina ovale formed by anteromedial struts of the alisphenoid tympanic wing, more carnassialized molars, and premolariform lower canines. Individual species of *Gracilinanus* differ from *H. kalinowskii* in other respects, but only *G. emiliae* merits explicit comparison here.

Gracilinanus emiliae occurs sympatrically with *H. kalinowskii* at Paracou, and because these species are similar in size and coloration (both have reddish dorsal fur and self-colored whitish venters), they might be confused in the field. However, numerous external characters permit unambiguous discrimination. *Gracilinanus emiliae* differs from *H. kalinowskii* in facial markings (its black fa-

cial mask does not extend to the base of the ear, and the streak of orange fur between its eyes is darker and narrower) and has smaller ears, smaller manual claws (not extending beyond the fleshy digital pads), 4–1–4 = 9 mammae, and a much longer tail with smaller scales and no trace of lighter banding over the vertebral articulations. Another external character that might distinguish *G. emiliae* and *H. kalinowskii* is the presence/absence of gular glands, but the variability of this trait within species is not well documented and, with so few examples available for comparison, its diagnostic value is uncertain. The skull of *G. emiliae* differs from that of *H. kalinowskii* in the cranial characters listed above for *Gracilinanus* and by the presence of a posterior accessory cusp on the upper canine (a trait not consistently exhibited by other congeners).

Members of other "marmosine" genera differ consistently from *Hyladelphys* by their larger size and size-correlated proportions (relatively longer rostrums, smaller orbits, less inflated braincases) and in the following qualitative contrasts (in addition to the mammary and milk-dentitional traits mentioned previously): incrassate tails (*Thylamys*), grossly enlarged central hairs of each caudal-scale triplet (*Marmosops*), distinct postorbital frontal processes (*Marmosa, Micoureus*), secondary foramina ovale (*Marmosops, Thylamys*), I2–5 conspicuously increasing in size from front to back (*Marmosops* and some *Marmosa*), P3/p3 larger than or subequal to P2/p2 (*Thylamys*), more carnassialized molars (all genera), and premolariform c1 (*Marmosops*). Insofar as can be inferred from polyprotodont character polarities (e.g., as hypothesized by Archer, 1976a, 1976b; Creighton, 1984; Reig et al., 1987; Wroe, 1997), *Hyladelphys* shows no clear pattern of synapomorphic resemblances with any other didelphid taxon. By the same token, evidence of a closer relationship to nondidelphid clades is also weak. In effect, our assignment of *Hyladelphys* to the family Didelphidae is based primarily on zoogeography and on morphological traits that are currently interpreted as marsupial plesiomorphies.

Remarks: A published portrait of the head of *Hyladelphys kalinowskii* reconstructed from dried skins (Hershkovitz, 1992: fig. 14) is misleading in several details. The bulging eyes of our fluid-preserved specimens are proportionately about twice as large as those in the drawing. The pinnae in the illustration are shown bristling with short hairs, but the auricular pelage is actually microscopic and the unmagnified ears appear quite naked; the ears in life are also proportionately much larger than drawn. The portrait does not show the genal vibrissae, but these long black hairs are conspicuous against the short white fur of the cheeks in all of the specimens at hand. The mystacial vibrissae are depicted as fine, inconspicuous hairs that extend only to the outer canthus of the eye, but these robust whiskers actually extend nearly to the tips of the pinnae when laid back along the side of the head. The facial markings in the portrait also lack the vivid definition characteristic of this species: the mask is intensely black in fresh specimens and is boldly accentuated by a broad streak of very pale orange fur down the midline of the rostrum.

We examined the western Ecuadorean specimen (KU 135097) that Hershkovitz (1992: 42) identified as "*Gracilinanus* sp. (new species)" and that he subsequently (op. cit.: 45) conjectured ". . . is most nearly like adult *Gracilinanus kalinowskii* . . . ". The animal in question is a juvenile male (not a female as originally reported) preserved in fluid with an extracted skull, of which the first upper molar (crown length = 2.26 mm) suggests an adult size far larger than that of *Hyladelphys* or any known species of *Gracilinanus.* The large size of its caudal scales, absence of posteromedial palatal vacuities, and absence of an anteromedial alisphenoid strut bridging the foramen ovale are additional traits that cannot be reconciled with Gardner and Creighton's (1989) diagnosis of *Gracilinanus.* From *Hyladelphys,* KU 135097 differs conspicuously by its well-developed rostral process of the premaxillae, well-developed postorbital jugal process, upper incisor morphology (I1–5 have large, overlapping, symmetrically rhomboidal crowns that increase in size from front to back), fully molariform dP3, and highly carnassialized molars. Based on these and other attributes, we refer this specimen to the genus *Marmosa* (sensu Gardner and Creighton, 1989), within which it most closely resem-

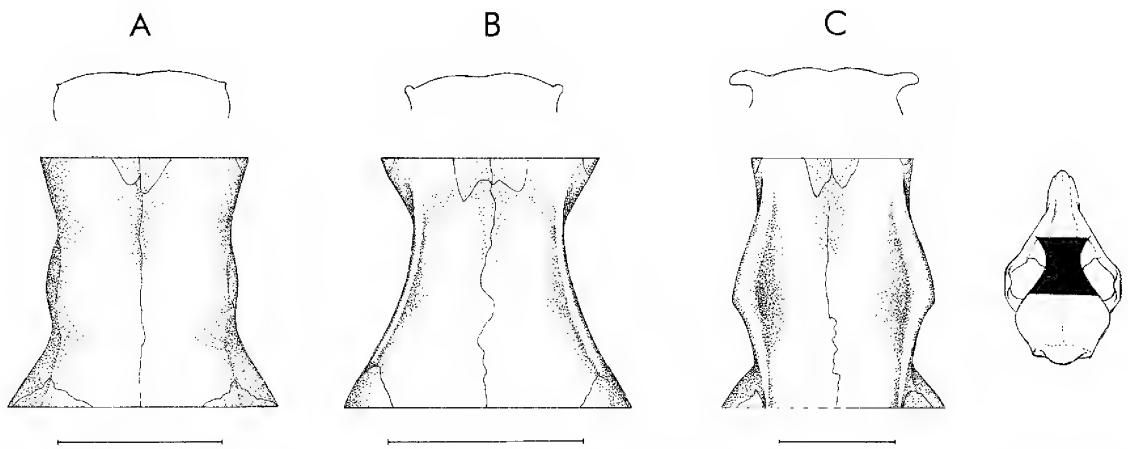

Fig. 19. Cross-sections and dorsal views of the interorbital regions of some Paracou marsupials: (**A**) *Marmosops pinheiroi* (AMNH 267341), (**B**) *Hyladelphys kalinowskii* (AMNH 267339), (**C**) *Marmosa murina* (AMNH 267368). Whereas the interorbital region of *Marmosops parvidens* is "hourglass-shaped" in dorsal view and has more-or-less rounded supraorbital margins, the interorbital region is "convergent" in *Hyladelphys kalinowskii* and has well-developed supraorbital beads. Adult specimens of *Marmosa murina* are characterized by large, triangular postorbital processes. All scale bars = 5 mm.

bles *M. mimetra* Thomas (1921) and other nominal taxa currently synonymized (Gardner, 1993) with *M. robinsoni.*

Other Specimens Examined: **Guyana**—*East Berbice-Corentyne,* New River Falls (ROM 34271). **Peru**—*Cuzco,* Hacienda Cadena (FMNH 8991 [type]); *Junín,* Chanchamayo (FMNH 65754 [paratype]); *Loreto,* Río Gálvez, Nuevo San Juan (MUSM 11031).

Field Observations: Our first example of this species from Paracou (MNHN 1995.903) was shot as it perched on a palm frond about 1 m above the ground in swampy primary forest at 18:35 hours on 25 October 1992. The other two specimens (AMNH 267338, 267339) were taken from the same pitfall trapline, near a small stream in well-drained primary forest, on 21 August 1993.

Marmosa murina (Linnaeus)

Figures 7, 19C, 21B

Voucher Material: AMNH 266416, 266417, 267368, 267816; MNHN 1995.904. Total = 5 specimens.

Identification: Our vouchers conform closely in all essential details of external and craniodental morphology with Tate's (1933) and Husson's (1978) authoritative descriptions of this species, the type locality of which was restricted by Thomas (1911a) to Surinam. According to Tate (1933: 95), two subspecies are parapatrically distributed in Surinam and French Guiana: supposedly, *Marmosa murina murina* ranges "along the narrow coastal strip between the sea and the heavy rainforest", whereas "in the rainforest it is replaced by the smaller darker [*M. m.*] *muscula* [(Cabanis)]." Husson (1978), however, recognized only the former taxon in his Surinamese material, and all of the Surinamese specimens that we examined appear to represent a single recognizable form—closely conforming to Husson's description and resembling our Paracou vouchers in qualitative characters and measurements (table 6)—that we assume to represent typical *M. murina.* Unfortunately, possible character differences between the types of *murina* and *muscula* are now difficult to evaluate.

Thomas (1892) identified two syntypes of *Didelphys murina* Linnaeus (1758) among the specimens of the Lidth de Jeude collection purchased by the BMNH in 1867. One of these (BMNH 67.4.12.542) was designated as the lectotype by Husson (1978), but his choice was unfortunate: the lectotype is a fluid-preserved adult female from which the skull has been extracted and apparently lost. The skull of the adult male paralectotype

TABLE 6
Measurements (mm) and Weights (g) of Adult *Marmosa murina* from French Guiana and Surinam

	Paracou vouchers					
	AMNH 267816	AMNH 266416	AMNH 267368[a]	Paralecto-type[b]	Topotypes[c]	
Sex	male	female	?	male	males[d]	females[e]
HBL	120	122	—	—	141 (132–152) 6	126 (118–137) 7
LT	192	172	—	—	183 (175–195) 5	164 (156–172) 7
HF	21	19	—	23	21 (20–23) 6	19 (16–21) 7
Ear	22	23	—	—	23 (21–25) 6	22 (21–23) 7
CBL	33.9	32.2	36.7	—	35.1 (33.5–37.2) 6	32.9 (31.9-34.2) 7
LM	6.7	7.1	6.8	6.8	6.6 (6.4–6.9) 6	6.6 (6.3–6.9) 7
PB	10.8	11.1	11.2	11.3	11.0 (10.7–11.8) 6	10.8 (10.2–11.3) 7
PL	19.2	18.2	20.7	20.5	19.5 (18.4–21.0) 6	18.5 (17.6–19.0) 7
LIB	5.9	5.8	6.5	6.3	6.3 (6.0–7.3) 6	5.6 (5.4–6.0) 7
ZB	18.7	18.5	19.8	—	20.3 (19.3–22.3) 6	18.8 (18.2–20.0) 7
Wt	46	45	—	—	61 (55–80) 5	42 (35–50) 5

[a] Skull only.

[b] BMNH 67.4.12.541, collection locality unknown, but presumed to be from Surinam.

[c] From Surinam (Thomas, 1911a). Measured specimens were collected within 100 km of Paramaribo. The sample mean, observed range (in parentheses), and sample size are provided for each measurement.

[d] FMNH 95315, 95321, 95322, 95324, 95326, 95328.

[e] CM 68346, 68353; FMNH 95323, 95325, 95329, 95330, 95332.

(BMNH 67.4.12.541), however, has measurements that fall within the range of variation that we observed among recently collected specimens from Surinam (table 6). Tate (1933) described the pelage color of BMNH 67.4.12.541 in considerable detail, but neither this specimen nor the lectotype are really suitable for subspecific color comparisons because their pigments may have faded after more than two centuries in alcohol.

The holotype of *Marmosa murina muscula* (type locality: "Caraiben Niederlassung Arrai am obern Pomeroon" [Cabanis, 1848: 778], Pomeroon-Supenaam, Guyana) is a juvenile specimen (with dP3 in place and M4 unerupted) that consists of the skin and skull of an animal originally preserved in fluid. Because of its immaturity, and because the pelage is now faded from preservative and discolored by age, the type of *muscula* is likewise unsuitable for subspecific comparisons. A small series of skins from Kartabo, Guyana, that Tate (1933) identified as *M. m. muscula,* however, are dorsally somewhat darker than our Paracou vouchers, but have whiter venters with less extensive lateral zones of gray-based fur. Whereas the dorsal color difference is consistent with Tate's diagnosis of *muscula* versus *murina,* the ventral color difference is not. The only qualitative cranial character cited by Tate as diagnostic of *muscula,* the absence of dorsal grooves along the supraorbital ridges, is apparently useless for defining this taxon (as represented by Tate's own identifications) inasmuch as all the fully adult skulls from the Kartabo series (AMNH 42908, 48135, 99983, 142807) have grooved supraorbital ridges. Given that (1) the other character differences between *murina* and *muscula* cited by Tate are indefinite, (2) that the relevant types have discolored pelage and are incommensurate in age, and (3) that the material we examined from Surinam and French Guiana shows no appreciable divergence in size or coat color between coastal and interior populations, it does not seem useful to recognize these subspecies as valid at the present time.

We also examined the types of other nominal taxa from the Guiana subregion of Amazonia currently treated as subjective synonyms of *Marmosa murina,* including *klagesi*

Allen (1900), *chloe* Thomas (1907), *roraimae* Tate (1931), and *duidae* Tate (1931). All of these are chiefly distinguishable by pelage characters—subtle differences in fur color, length, and texture—that perhaps vary clinally with environmental conditions as suggested by Tate himself (1933, 1939), who ranked them as no more than subspecifically distinct. By contrast, the conspecificity of some taxa from outside the Guiana subregion that are currently referred to *M. murina* (e.g., by Gardner, 1993) is more problematic. For example, *M. quichua* Thomas (1899a) from western Amazonia is craniodentally distinctive (Tate, 1933; personal obs.) and no justification for its synonymy with *M. murina* has apparently been published. In view of the lack of any critical review of the species-level taxonomy of *Marmosa* (sensu stricto) since Tate's 1933 monograph, that work should still be considered the primary authority for species limits until compelling evidence is provided for alternative classifications.

Other Specimens Examined: **French Guiana**—Arataye (MNHN 1981.172, 1981.173, 1982.597, 1986.125), Cayenne (MNHN 1986.1024, 1986.1025), Les Nouragues (MNHN 1998.307), Piste St.-Élie (MNHN 1981.417–1981.419, 1981.421, 1981.422, 1982.598), Saül (MNHN 1982.596, 1986.484). **Guyana**—"Demerara River 29 miles above Georgetown" (BMNH 7.6.20.16 [holotype of *chloe*]); *Cuyuni-Mazaruni,* Kartabo (AMNH 42907, 42908, 48135, 99983, 142807); *Pomeroon-Supenaam,* "Caraiben-Niederlassung Arrai am obern Pomeroon" (ZMB 2331 [holotype of *muscula*]). **Suriname**—*Brokopondo,* Finisanti (FMNH 95315–95319, 95321–95326, 95328); *Marowijne,* Oelemarie (CM 76729); *Para,* Zanderij (CM 68346, 68353); *Saramacca,* Raleigh Falls (CM 68354, 68355, 68356); *Suriname,* Lelydorpplan (FMNH 95329, 95330, 95332). **Venezuela**—*Amazonas,* Mt. Duida (AMNH 76984 [holotype of *duidae*]); *Bolívar,* Ciudad Bolívar (AMNH 16121 [holotype of *klagesi*]), Arabupu (AMNH 75703 [holotype of *roraimae*]). **Without locality data**—(BMNH 67.4.12.541 [paralectotype of *murina*], 67.4.12.542 [lectotype of *murina*]).

Field Observations: All of our records of *Marmosa murina* at Paracou are based on specimens collected in secondary growth and other manmade habitats: two were shot at night as they perched 1–2 m above the ground in dense roadside vegetation, one was caught by hand at night in a garden, and two were found killed and partially eaten (probably by domestic cats) near houses in clearings.

Marmosops Matschie

Thirty-five voucher specimens from Paracou are referable to *Marmosops parvidens* in the sense of Pine (1981), but close examination of pelage characters and correlated morphometric variation in our sample indicates that two species are present. The following paragraphs summarize the evidence supporting this conclusion.

All of the specimens in question are small opossums (21–33 g adult weight) with dark facial masks, dull reddish-brown or grayish-brown dorsal fur, small fore- and hindfeet (each with diminutive claws and six separate plantar tubercles), and long tails. The scrotal sacs of males are entirely white. Female specimens lack any trace of a pouch and appear to have have 3–1–3 = 7 or 4–1–4 = 9 inguinal-abdominal mammae (fig. 15B). Other distinctive attributes include: the grossly enlarged central hair of each caudal-scale triplet; a prominent, spoon-shaped, fleshy tubercle supported internally by bone on the lateral aspect of the wrist of males (fig. 20); smoothly rounded supraorbital margins without distinct beads or processes (fig. 19A); conical alisphenoid bullae with prominent anteromedial processes (fig. 21); absence of posteromedial (palatine) palatal vacuities (fig. 22); upper canines with distinct anterior and posterior accessory cusps; and lower canines that resemble the lower premolars in shape and size, forming a more-or-less undifferentiated series of four subequal teeth (fig. 23). Some of these traits are common to many "marmosines", others are perhaps diagnostic of the genus *Marmosops,* and a few may define a distinctive group of species closely related to *M. parvidens.* For present purposes, however, these attributes serve to distinguish examples of *parvidens*-like *Mar-*

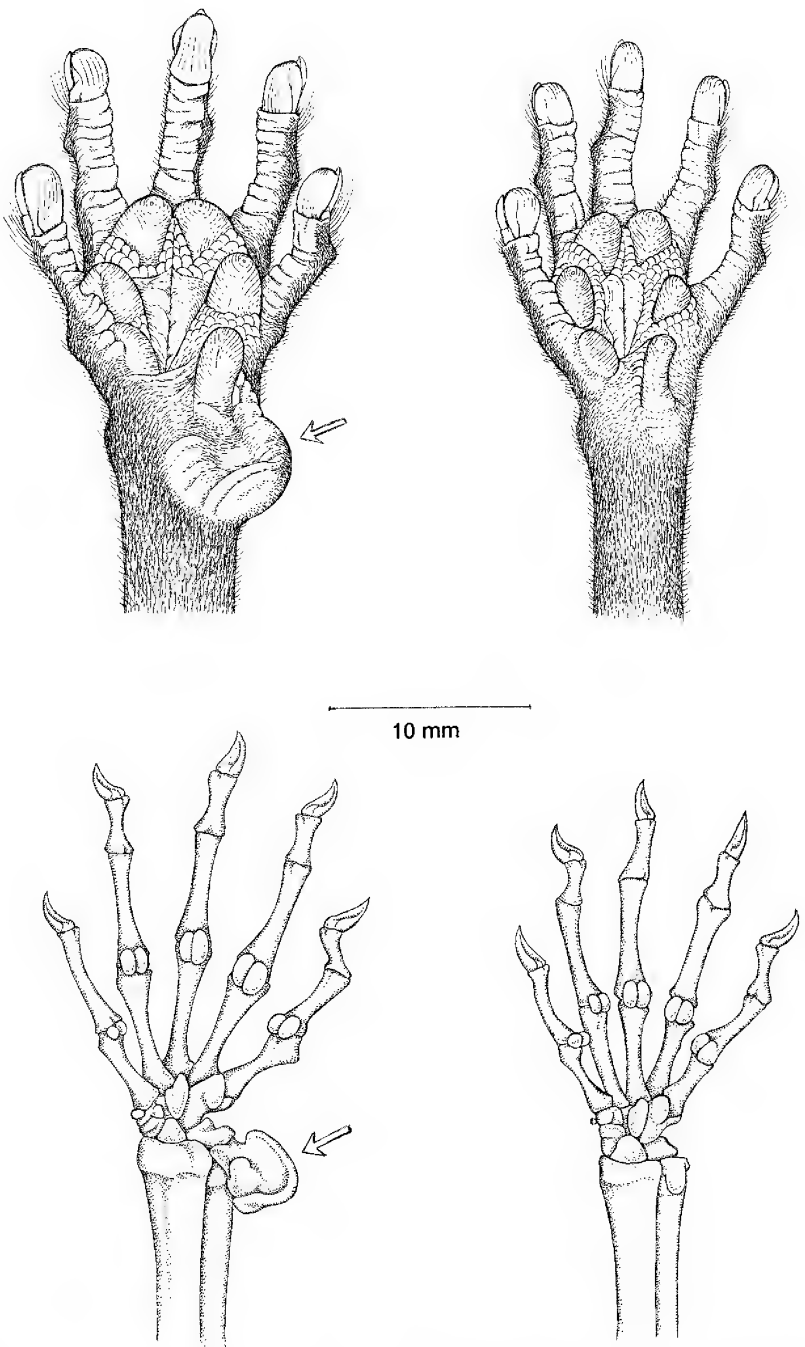

Fig. 20. Sexually dimorphic wrist morphology of members of the *Marmosops parvidens* species group. Adult males (left) possess an externally obvious lateral carpal tubercle that is supported internally by an enlarged pisiform bone (arrows); females (right) do not show this character (see Lunde and Schutt, 1999, for further details). *Marmosops parvidens* and *M. pinheiroi,* both members of the Paracou fauna, have similar wrist morphologies, but males of other taxa referable to the *M. parvidens* species group (e.g., *M. juninensis,* see text) differ in the size and shape of the lateral carpal tubercle. Illustrated specimens are examples of *Marmosops pinheiroi* from Paracou: top and bottom left, AMNH 267346; top and bottom right, AMNH 267342.

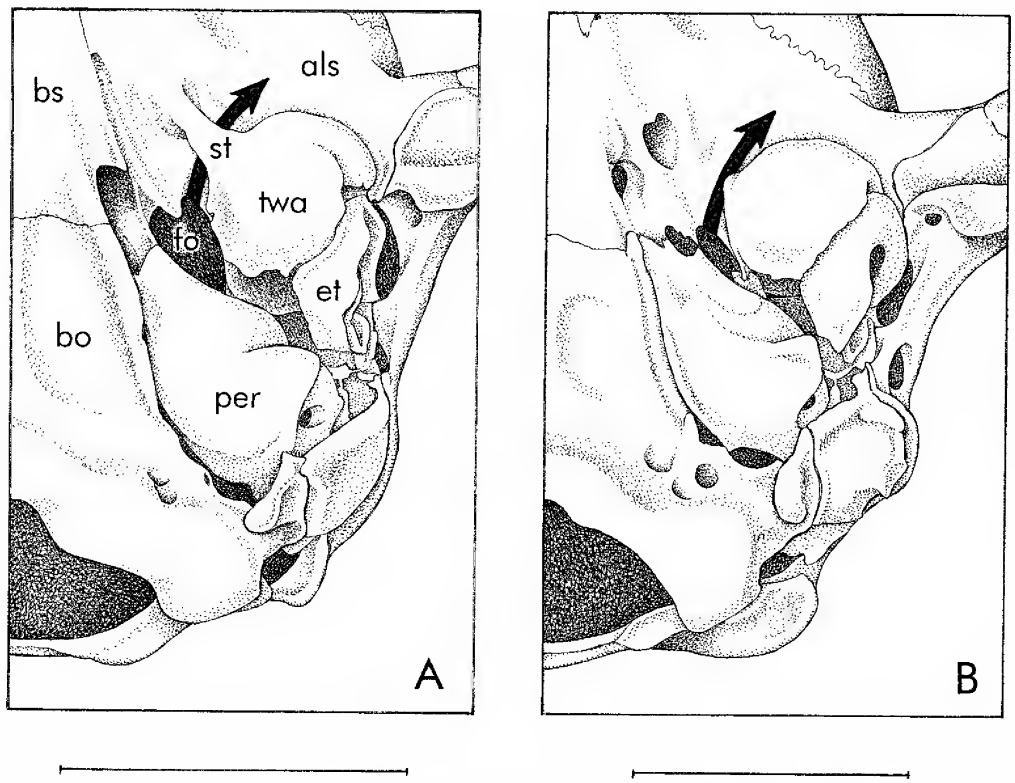

Fig. 21. Detail of auditory region in (**A**) *Marmosops pinheiroi* (AMNH 267346) and (**B**) *Marmosa murina* (AMNH 267368). In *Marmosops,* the tympanic wing of the alisphenoid (**twa**) produces an anteromedial strut (**st**) that partially encloses the mandibular branch of the trigeminal nerve (V^3, reconstructed course shown by heavy arrow); the nerve then emerges from a secondary foramen ovale. In *Marmosa,* the extracranial course of the nerve is unenclosed by the alisphenoid because the anteromedial strut is absent; there is no secondary foramen ovale in this species. Other abbreviations: **als,** alisphenoid; **bo,** basioccipital; **bs,** basisphenoid; **et,** ectotympanic; **fo,** foramen ovale; **per,** periotic.

mosops from all of the other marsupial taxa that we collected at Paracou.

Within this series, the most conspicuous external variation involves fur color. We scored three pelage characters for statistical analysis. *Dorsal coloration* was classified as "fuscous" (dusky grayish-brown) or "reddish" (a subtly warmer tone) according to the predominant hue of the unruffled fur. Although this chromatic contrast disappears in material stored for years in alcohol, dried skins and fresh fluid specimens (recently removed from formalin) were readily assigned to one or the other of these two states.[7] *Ventral coloration* was classified as "white" if the self-colored fur and the tips of gray-based hairs lacked any pigmentation, or "cream" if the self-colored fur and gray-based hair tips were pale yellowish. *Ventral pattern* was classed as "narrow" if self-colored (pure white or cream) fur was confined to the midline (sometimes as a discontinuous streak) by a broad zone of gray-based fur on each side, "broad" if almost the entire ventrum was self-colored, or "intermediate" for speci-

[7] At the time of writing (1997), specimen assignments to dorsal and ventral color classes (recorded in 1993) are difficult to verify in fluid-preserved material (the bulk of our vouchers) due to fading. Five dried skins, however, retain their original colors: AMNH 266423, 267007, and 267352 have "fuscous" dorsal fur and "white" underparts; AMNH 266426 has "reddish" dorsal fur and "cream" underparts; and AMNH 267817 has "reddish" dorsal fur and "white" underparts. The extent of gray-based ventral fur (another pelage character we scored for statistical analysis) is not affected by ageing or preservatives.

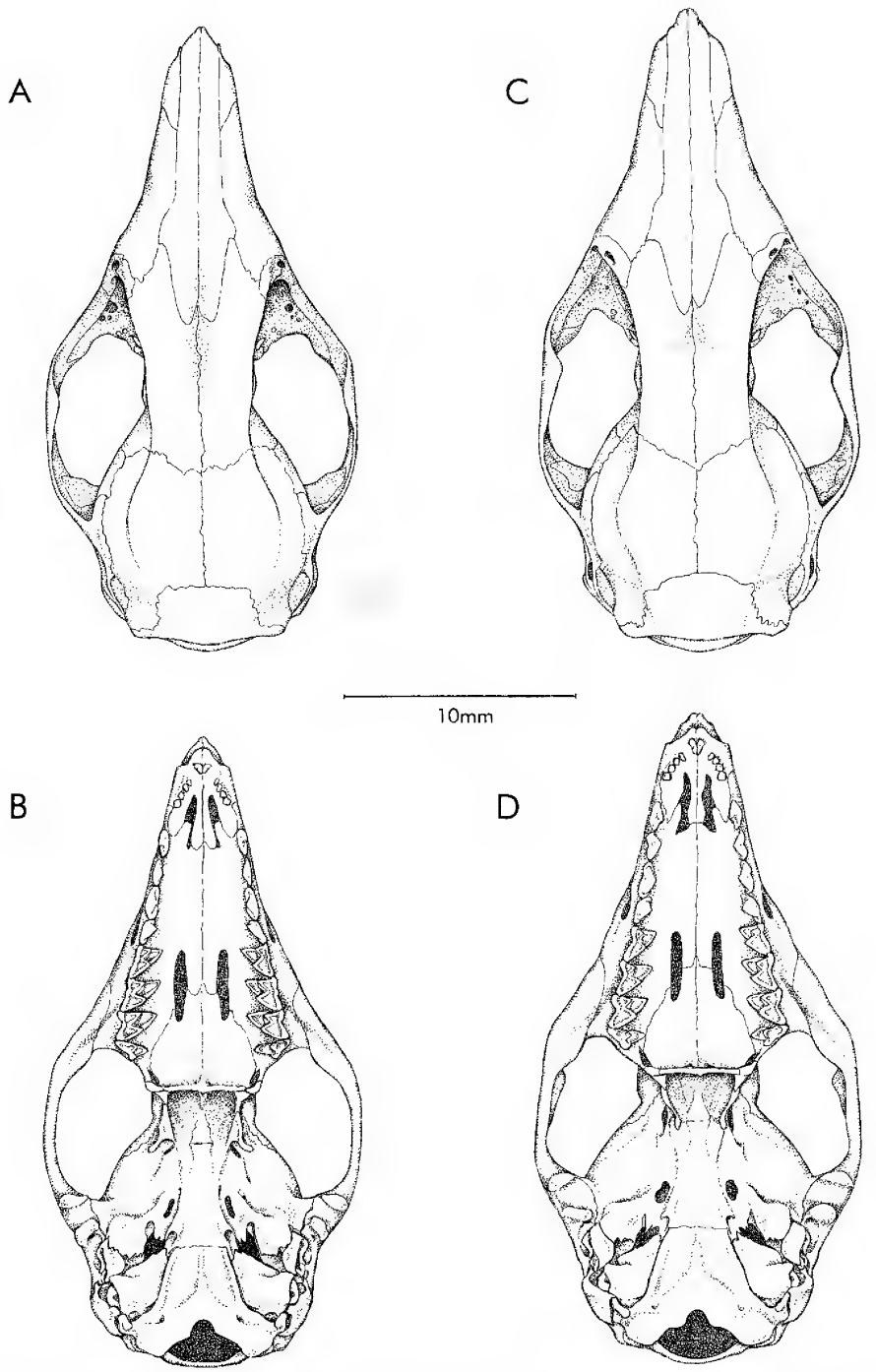

Fig. 22. Dorsal and ventral cranial views of (**A, B**) *Marmosops parvidens* (AMNH 267359, male) and (**C, D**) *M. pinheiroi* (AMNH 267345, male). Note species differences in size and in the relative breadth of the rostrum.

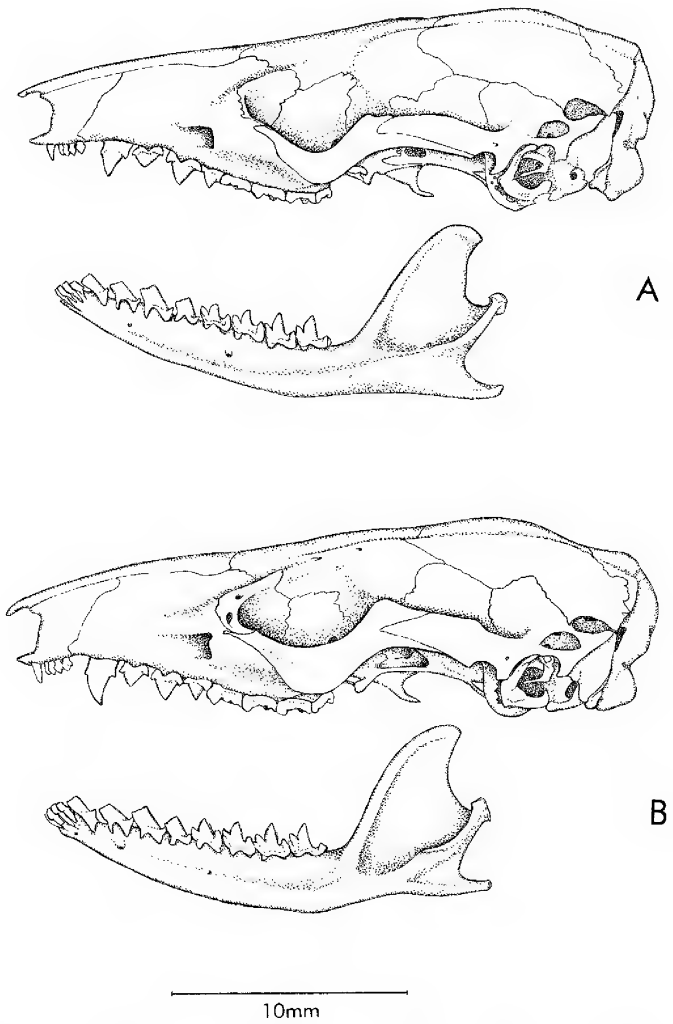

Fig. 23. Lateral views of crania and mandibles of (**A**) *Marmosops parvidens* and (**B**) *M. pinheiroi* based on the same specimens as in figure 22. Note the smaller upper canine of *M. parvidens.* The premolariform lower canines (forming a continuous series of four subequal teeth with p1–3) distinguish both species from other sympatric marmosines.

mens with substantial amounts of both self-colored and gray-based ventral fur.

Chi-squared tests of independence provide no evidence for age or sex effects on the expression of these pelage traits. In fact, the largest age-sex class in our sample (16 adult males) includes individuals with fuscous and reddish dorsal fur, specimens with white and cream-colored ventral fur, and examples of all three conditions of ventral pattern. However, pelage characters are not independently distributed inter se (table 7). Most animals with fuscous dorsal fur have self-colored ventral fur narrowly confined to the midline or bordered by extensive lateral zones of gray-based fur; by contrast, many animals with reddish dorsal fur have almost entirely self-colored ventral fur, and none has self-colored fur narrowly confined to the midline. Similarly, almost all animals with fuscous dorsal fur have white (or white-tipped) ventral fur, whereas about one-third of the specimens with reddish dorsal fur have cream (or cream-tipped) underparts.

We used one-way ANOVAs to test for morphometric divergence between individu-

TABLE 7
Chi-Square Tests for Independence of Pelage Characters[a] among *Marmosops* Specimens from Paracou

		VENTRAL PATTERN			
		Broad	*Inter-mediate*	*Narrow*	Totals
DORSAL COLOR	*Fuscous*	1	9	9	19
	Reddish	9	5	0	14
	Totals	10	14	9	33

$\chi^2 = 16.2$, df = 2, $p \ll 0.01$[b]

		VENTRAL COLOR		
		Cream	*White*	Totals
DORSAL COLOR	*Fuscous*	1	18	19
	Reddish	5	9	14
	Totals	6	27	33

$\chi^2 = 5.0$, df = 1, $p < 0.03$[b]

[a] See text for character definitions. Table entries are numbers of specimens cross-classified for row and column traits. Two specimens (out of 35 total) were too ant-damaged to score for pelage characters.

[b] Test may be biased by small expected frequencies in some cells.

als with red and fuscous dorsal fur among adult males (the only age-sex class in our sample large enough for such analyses) and found highly significant differences ($p < 0.01$) in length of molars, palatal breadth, zygomatic breadth, height of the upper canine (measured from the posterior accessory cusp to the tip of unworn teeth), and nasal breadth. Other external and craniodental measurements showed no significant divergence. Not surprisingly, principal components analysis of the log-transformed craniodental measurement data provides clear separation of dorsal fur color classes aligned with the first eigenvector (fig. 24), the coefficients of which (table 8) reflect essentially the same differences as those indicated by univariate statistics: fuscous adult males have taller canines, broader nasals, and wider zygomas than do reddish adult males, with smaller (but still substantial) differences in molar size and palatal breadth. Similar morphometric contrasts between dorsal fur color classes can be seen among the few adult females in our sample, and among immatures.

Close inspection of skulls revealed another difference between the two groups of specimens previously sorted by chromatic and morphometric traits. In specimens with fuscous dorsal fur, taller canines, and broader skulls, the lacrimal bone forms a prominent part of the anteroventral margin of the orbit; the lacrimal foramina then perforate the orbital margin, where they are exposed in lateral view (fig. 25B). By contrast, the lacrimal bone is not a prominent part of the anteroventral orbital margin in specimens with reddish dorsal fur, smaller teeth, and narrower skulls; in these, the lacrimal foramina are always located within the orbit, where they are more-or-less concealed from lateral view (fig. 25A).

We interpret the correlation between pelage characters, morphometric differences, and lacrimal morphology described above as evidence that two species of *Marmosops* are sympatric at Paracou. Based on our examination of relevant type material (see below), we identify the reddish individuals with shorter canines, narrower skulls, and reduced lacrimals as *M. parvidens,* and the fuscous individuals with taller canines, broader skulls, and prominent lacrimals as *M. pinheiroi.* A single Paracou specimen (AMNH 267358), consisting of the skeleton only of a juvenile animal with a smashed skull, is not assignable with certainty to either species.

Marmosops parvidens (Tate)
Figures 15B, 22A, 22B, 23A, 25A, 26A

VOUCHER MATERIAL: AMNH 266425, 266426, 267344, 267347, 267348, 267350, 267353, 267359, 267361, 267817; MNHN 1995.927–1995.930, 1995.933. Total = 15 specimens.

IDENTIFICATION: Specimens of *Marmosops parvidens* can be distinguished from sympatric examples of *M. pinheiroi* at Paracou by their warmer (more reddish) dorsal fur, broader extent of self-colored fur (which is never discontinuous between chin and anus), smaller teeth (especially upper canines), narrower skull, and by the reduced lacrimal contribution to the anteroventral orbital margin (see above). Because the difference in dorsal pelage color is subtle, and because there is some overlapping variation in the extent of self-colored ventral fur, unambiguous species

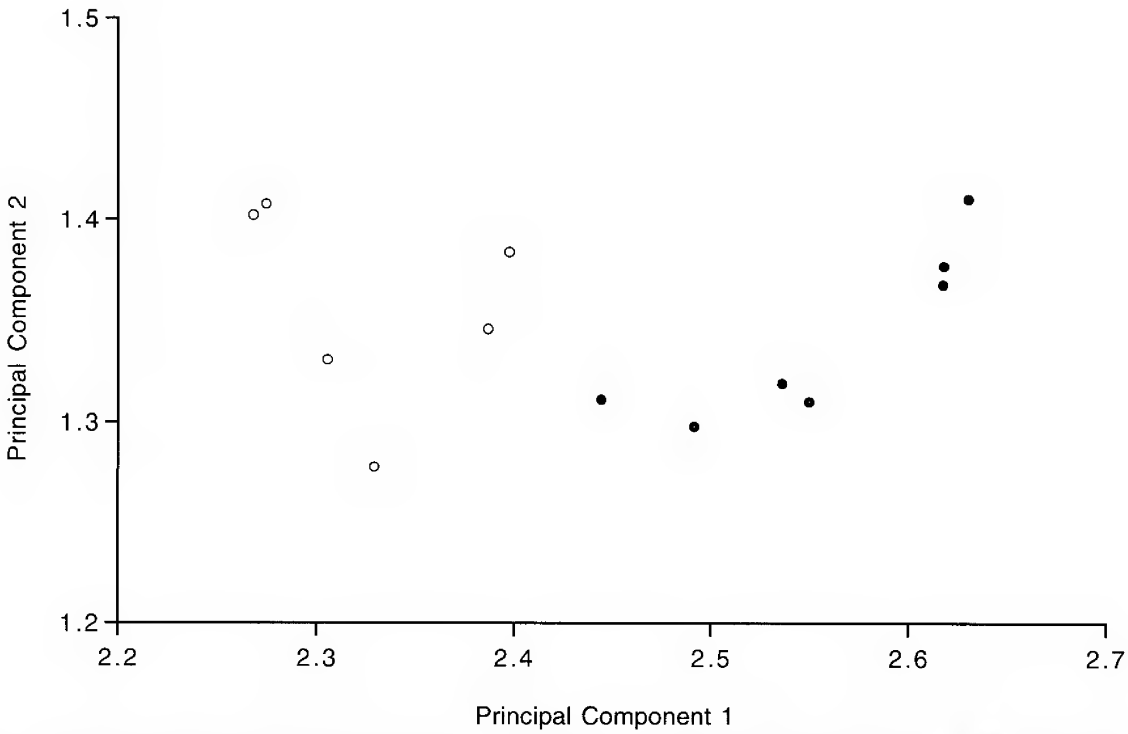

Fig. 24. Specimen scores of adult male *Marmosops parvidens* (○) and *M. pinheiroi* (●) on the first two principal components extracted from the covariance matrix of eight log-transformed craniodental measurements (see text). Variable coefficients and eigenvalues (scaled as percentages of the total variance in these data) are provided in table 8.

TABLE 8

Principal Components Analysis of Craniodental Measurement Variation among 16 Adult Male *Marmosops* from Paracou[a]

	Eigenvectors	
	PC1	PC2
Coefficients		
Condylobasal length	0.102	0.073
Length of molars	0.119	−0.031
Palatal breadth	0.113	−0.360
Palatal length	0.074	0.090
Least postorbital breadth	0.039	0.421
Zygomatic breadth	0.174	0.088
Height of canine[b]	0.745	−0.519
Nasal breadth	0.609	0.633
% Variance	77.8	8.8

[a] Principal components were extracted from the variance–covariance matrix of measurements transformed to their natural logarithms. Specimen scores are plotted in figure 24.

[b] Measurement defined in accompanying text.

identifications require cleaned cranial material. In our voucher series, height of canine (HC) affords the clearest discrimination (tables 9, 10), but toothwear and sexual dimorphism must be taken into account in sorting specimens by this criterion. Lacrimal morphology (fig. 25) is perhaps the most reliable cranial character for identifying juveniles with incompletely erupted (and therefore unmeasurable) canines.

Although a revision of what may be called the *parvidens* group of *Marmosops* is beyond the scope of this faunal report, we note that our conclusion that two species assignable to this complex are sympatric at Paracou is consistent with recent molecular evidence that *M. parvidens* sensu Pine (1981) is composite (Mustrangi and Patton, 1997; Patton et al., 2000). In addition to recognizing *M. pinheiroi* as a valid species, we note that *M. juninensis* (another "subspecies" of *M. parvi-*

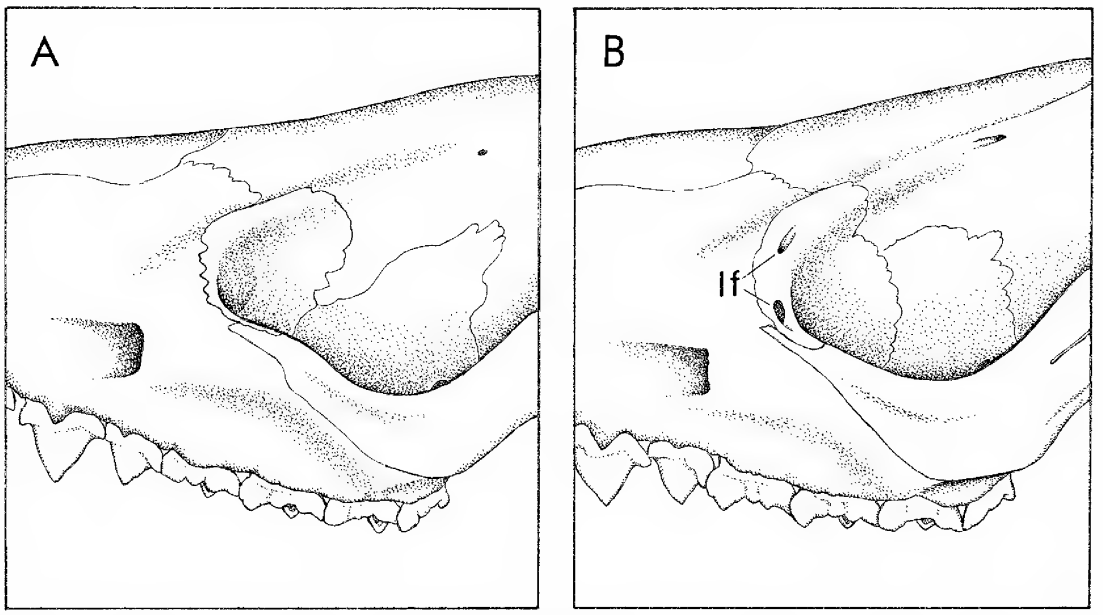

Fig. 25. Detail of the anterior orbital region in (**A**) *Marmosops parvidens* and (**B**) *M. pinheiroi* based on the same specimens as in figures 22 and 23. In *M. parvidens* the lacrimal bone does not form a large part of the orbital margin, and the lacrimal foramina are concealed from lateral view inside the orbit. In *M. pinheiroi* the lacrimal bone forms a larger part of the orbital margin, and the lacrimal foramina (**lf**) are laterally exposed.

dens sensu Pine, 1981) is equally distinctive and also merits specific recognition. Originally described by Tate (1931) on the basis of a single specimen (AMNH 63864), *M. juninensis* (now additionally represented by AMNH 230014–230016, all collected near Tarma in Depto. Junín, Peru) can be unambiguously distinguished from *M. parvidens* (sensu stricto) and *M. pinheiroi* by the size and shape of the male carpal tubercle (smaller and not spoon-shaped), by the consistent presence of posteromedial palatal vacuities, and by the absence of distinct accessory cusps on the upper canine (fig. 26). Like *parvidens,* but unlike *pinheiroi,* the lacrimal bone in *juninensis* does not form part of the anteroventral orbital margin, so the lacrimal foramen lies inside the orbit. Unlike any specimens of *parvidens,* however, the ventral pelage of *juninensis* is entirely gray-based.

We examined the type of *Marmosops parvidens bishopi* (USNM 393535), the pelage of which Pine (1981) described as colored essentially like that of *M. p. parvidens,* but paler. In our opinion, this specimen represents another distinct species that differs from *M. parvidens* in lacking any trace of an anterior accessory cusp on the upper canine. Specimens from Bolivia (e.g., AMNH 268938) and Peru (e.g., AMNH 67243) with darker (more saturated) dorsal fur than the type may nevertheless be provisionally referred to *M. bishopi* based on upper canine morphology.

A specimen from northern Venezuela (USNM 371299) that Pine (1981) referred to *Marmosops parvidens parvidens* lacks an anterior accessory upper canine cusp (like *M. bishopi*) and exhibits other differences from typical examples of *M. parvidens* as recognized in this report. The mystacial vibrissae of USNM 371299 appear to be very short, probably not extending much if at all beyond the base of the ear in life, whereas the mystacial hairs reach at least to the posterior margins of the pinnae in typical examples of *M. parvidens.* The dorsal fur of USNM 371299 is longer than in typical *M. parvidens* (about 9 mm middorsally versus about 7 mm), is fluffier in texture, and has a faintly marbled appearance that is not characteristic of other specimens that we refer to this species. Taken

TABLE 9
Measurements (mm) and Weights (g) of Adult Specimens of *Marmosops parvidens*

	Paracou vouchers		
	Males[a]	Female[b]	Holotype[c]
HBL	100 (93–107) 7	94	—
LT	149 (142–160) 7	138	—
HF	16 (15–17) 7	15	—
Ear	22 (21–24) 7	20	—
CBL	28.6 (27.6–29.2) 6	26.7	27.7
LM	5.5 (5.4–5.8) 8	5.5	5.4
PB	8.3 (8.1–8.7) 8	8.1	8.3
PL	16.1 (15.5–16.7) 7	15.1	15.9
LPB	5.5 (5.2–5.7) 7	5.3	5.7
ZB	14.6 (14.0–15.0) 7	13.9	14.9
HC[d]	1.08 (1.01–1.13) 8	1.01	1.00
NB	3.4 (3.2–3.7) 8	3.2	3.4
Wt	25 (21–31) 7	22	—

[a] The mean, the observed range (in parentheses), and the sample size are provided for the following series of specimens: AMNH 267347, 267348, 267353, 267359, 267361; MNHN 1995.929, 1995.930, 1995.933.

[b] AMNH 267344.

[c] FMNH 18545, female; from Hyde Park, Demerara-Mahaica, Guyana.

[d] Height of canine (see accompanying text), recorded to nearest 0.01 mm.

together, these differences suggest that USNM 371299 may represent an undescribed taxon, but more material should be examined to evaluate this conjecture.

With a single exception (AMNH 97333, see below), all of the specimens that we identify as *Marmosops parvidens* sensu stricto are from the Guiana subregion of Amazonia (fig. 27).

OTHER SPECIMENS EXAMINED: **Brazil**—*Amazonas,* Boca Rio Piratucu (AMNH 93970), 80 km N Manaus (USNM 579985–579990); *Pará,* Ilha do Taiuna on lower Rio Tocantins (AMNH 97333). **French Guiana**—Arataye (USNM 548439). **Guyana**—*Demerara-Mahaica,* Hyde Park (FMNH 18545 [holotype]); *Upper Takutu-Upper Essequibo,* Karanambo (ROM 97938).

FIELD OBSERVATIONS: Because unvouchered sightings of *Marmosops* could not be unambiguously identified to species, all of our definite records of *M. parvidens* at Paracou are from collected specimens. Five specimens of *M. parvidens* were shot, one was caught by hand, one was caught in a Victor trap, one in a Sherman trap, and the rest (seven) were captured in pitfalls; all were collected at night. Nine specimens were taken on the ground, five were found perching in understory vegetation (usually on vertical stems) 0.2–1.5 m above the ground, and one was trapped on a liana 1.8 m above the ground. Seven specimens were collected in well-drained primary forest, five in creekside primary forest, one in swampy primary forest, one in primary forest of unspecified character, and one in secondary growth.

See the following account for habitat comparisons between *Marmosops parvidens* and *M. pinheiroi.*

Marmosops pinheiroi (Pine)

Figures 16B, 19A, 20, 21A, 22C, 22D, 23B, 25B

VOUCHER MATERIAL: AMNH 266423, 266424, 267007, 267008, 267341–267343, 267345, 267346, 267349, 267351, 267352, 267354, 267357; MNHN 1995.925, 1995.926, 1995.931, 1995.932, 1995.934. Total = 19 specimens.

IDENTIFICATION: See the preceding account for diagnostic comparisons with *Marmosops parvidens.*

In addition to the holotype and paratypes of *Marmosops pinheiroi,* we examined the type series of *M. parvidens woodalli* (USNM 393529–393532, 393534, 545543), a subspecies that Pine (1981) described from the vicinity of Belém, Brazil. Although these specimens average paler dorsally than examples of *M. pinheiroi* from north of the Amazon, they are otherwise similar in pelage and craniodental characters, and we provisionally regard them as conspecific. An adult male specimen from the right bank of the lower Rio Xingu (USNM 549294), however, may represent an undescribed taxon. Although most of its qualitative traits match those of *M. pinheiroi,* it is much paler dorsally and has substantially smaller upper canines (HC = 1.06 mm) for its sex than any example of that species as recognized by us.

OTHER SPECIMENS EXAMINED: **Brazil**—*Amapá,* Serra do Navio (USNM 461459 [holotype], 461460, 461462–461465); *Pará,* Belém (USNM 545543), Utinga (USNM 393529–393532, 393534). **Guyana**—*Pota-*

TABLE 10
Measurements (mm) and Weights (g) of Adult Specimens of *Marmosops pinheiroi*

	Paracou vouchers		Type series[a]	
	Males[b]	Females[c]	Male[d]	Females[e]
HBL	104 (94–121) 8	101 (96–103) 3	105	100 (95–105) 5
LT	151 (142–156) 8	143 (137–152) 3	160	142 (135–150) 5
HF	17 (16–18) 8	16 (16–16) 3	—	—
Ear	22 (20–23) 8	19 (19–20) 3	—	—
CBL	29.1 (28.5–29.8) 8	28.0 (28.0–28.1) 2	29.8	28.8 (28.4–29.9) 5
LM	5.7 (5.6–5.9) 8	5.8 (5.7–5.8) 3	5.8	5.9 (5.5–6.2) 5
PB	8.7 (8.5–8.9) 8	8.6 (8.5–8.8) 2	8.9	8.9 (8.5–9.3) 5
PL	16.3 (16.0–16.7) 8	15.9 (15.8–16.0) 2	—	—
LPB	5.5 (5.2–5.8) 8	5.6 (5.4–5.7) 3	5.8	5.5 (5.3–5.6) 5
ZB	15.1 (14.6–15.6) 8	14.8 (14.7–15.0) 2	16.0	15.1 (15.0–15.3) 4
HC[f]	1.30 (1.22–1.35) 7	1.16 (1.13–1.19) 3	1.34	1.21 (1.08–1.29) 5
NB	3.8 (3.4–4.2) 8	3.6 (3.6–3.7) 2	3.8	3.1 (2.8–3.6) 5
Wt	29 (26–33) 8	23 (21–24) 3	27	21 (19–22) 5

[a] From Brazil: Amapá, Serra do Navio.

[b] The mean, observed range (in parentheses), and sample size are provived for the following series: AMNH 266423, 267341, 267345, 267346, 267349, 267357; MNHN 1995.931, 1995.932.

[c] The mean, observed range (in parentheses), and sample size are provided for the following series: AMNH 267342, 267352; MNHN 1995.934.

[d] USNM 461463.

[e] The mean, observed range (in parentheses), and sample size are provided for the following series: USNM 461459 (holotype), 461460, 461462, 461464, 461465.

[f] Height of canine (see accompanying text), recorded to nearest 0.01 mm.

ro-Siparuni, Iwokrama Reserve (ROM 108920). **Venezuela**—*Bolívar,* Auyan-tepui (AMNH 130521, 130568, 130570), Churi-tepui (AMNH 176352, 176353), 85 km SE El Dorado (USNM 385046).

FIELD OBSERVATIONS: All of our definite records of *Marmosops pinheiroi* at Paracou are from collected specimens. Four specimens were shot, three were captured in Victor traps, and the remainder (12 specimens) were caught in pitfalls; all were taken at night. Thirteen specimens were trapped or shot on the ground (one in a hollow log), but six were taken 0.3–1.5 m above the ground on vertical stems and lianas. Four specimens were collected in well-drained primary forest, five in creekside primary forest, six in swampy primary forest, and four in secondary growth.

Marmosops parvidens and *M. pinheiroi* clearly overlap in habitats at Paracou. Although our ecological classification is coarse and doubtless obscures many subtle differences among capture sites with the same descriptor (e.g., "well-drained primary forest"), we sometimes took both species in close proximity. One line of pitfall traps that traversed 50 m of apparently homogeneous primary forest along a small stream, for example, captured three *parvidens* and four *pinheiroi* between 29 July and 13 August 1993. Nevertheless, it is noteworthy that whereas we rarely took *parvidens* in swampy forest or secondary growth, over half of our *pinheiroi* specimens were collected in those habitats. Both species appear to occur only in the forest understory: no *Marmosops* were sighted or trapped at heights greater than about 2 m above the ground.

None of the adult female *Marmosops* we collected were carrying suckling young.

Metachirus nudicaudatus (E. Geoffroy)

VOUCHER MATERIAL: AMNH 266435, 266439, 266440, 266449, 266450, 266452, 266453, 266455, 267009, 267010, 267362, 267365; MNHN 1995.905–1995.910. Total = 18 (not including suckling young).

IDENTIFICATION: Our voucher material is al-

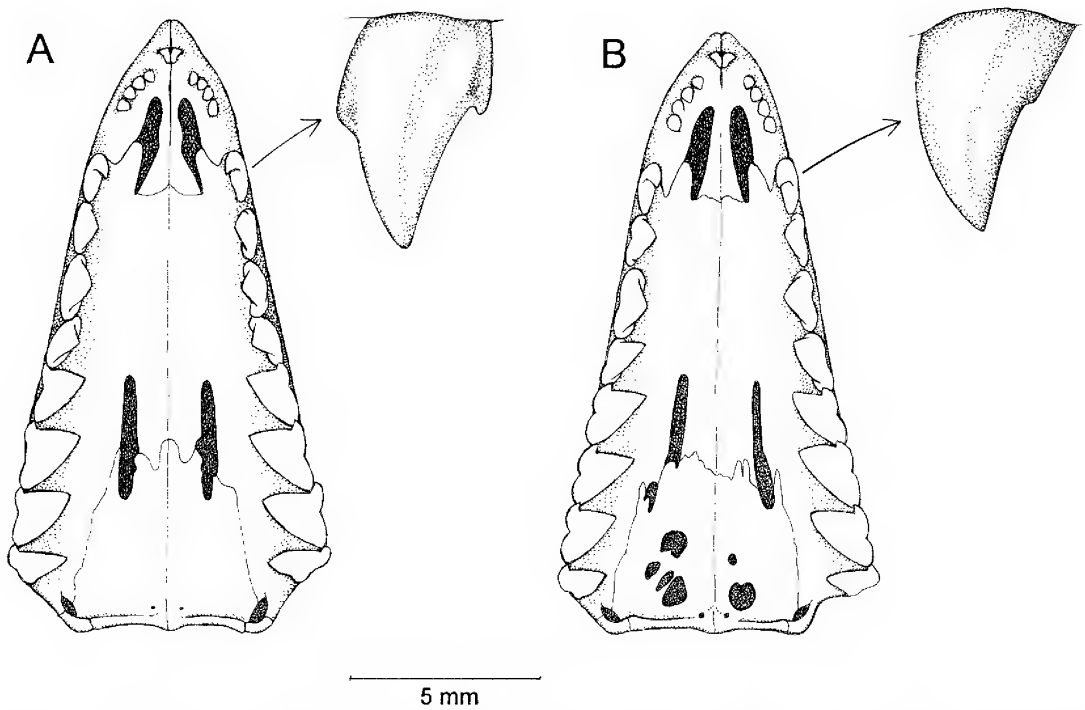

Fig. 26. Details of palatal and upper canine morphology of *Marmosops parvidens* (**A,** AMNH 267359) and *M. juninensis* (**B,** AMNH 230016). Among other differences between these distinctive species (see text), the posterior palate is more extensively fenestrated in *M. juninensis* than in *M. parvidens,* and *M. juninensis* lacks the distinct accessory cusps that are always present on the unworn upper canines of *M. parvidens.*

most topotypical of this species, which was originally described from a specimen collected at Cayenne (Julien-Laferrière, 1994). The Paracou series agrees closely in qualitative external characters with the description given by Husson (1978), and most craniodental measurements of the type fall within the range of metric variation in our voucher collection (table 11).

Although *Metachirus* has long been thought to contain but a single valid species (Tate, 1939; Cabrera, 1958; Gardner, 1993), this historical consensus is challenged by recently analyzed mtDNA sequences that suggest deep evolutionary divergence among samples from different Amazonian subregions (Patton et al., 2000). In the absence of any revisionary analysis of morphological specimens, however, it is unclear how mitochondrial haplotypes might correspond with named taxa. Inevitably, nominotypical material from French Guiana will play a pivotal role in any future attempt to resolve this unsatisfactory state of affairs.

Remarks: We agree with Julien-Laferrière (1994) that the name *Didelphis nudicaudata* is available from Geoffroy's (1803) catalog for the reasons explained by Hershkovitz (1955) and Holthuis (1963).

Other Specimens Examined: **French Guiana**—Cayenne (MNHN 1990.420 [holotype]).

Field Observations: We recorded 22 observations of *Metachirus nudicaudatus* at Paracou, of which 18 are based on collected specimens and 4 are unvouchered sightings. Eighteen records (82%) are of animals shot or sighted on the ground, but one specimen (4%) was trapped on the ground in a Tomahawk live trap, and three specimens (14%, all juveniles) were taken in Victor snap-traps tied to lianas 0.5–1.3 m above the ground. All of our records are from animals shot, sighted, or trapped at night. Fourteen indi-

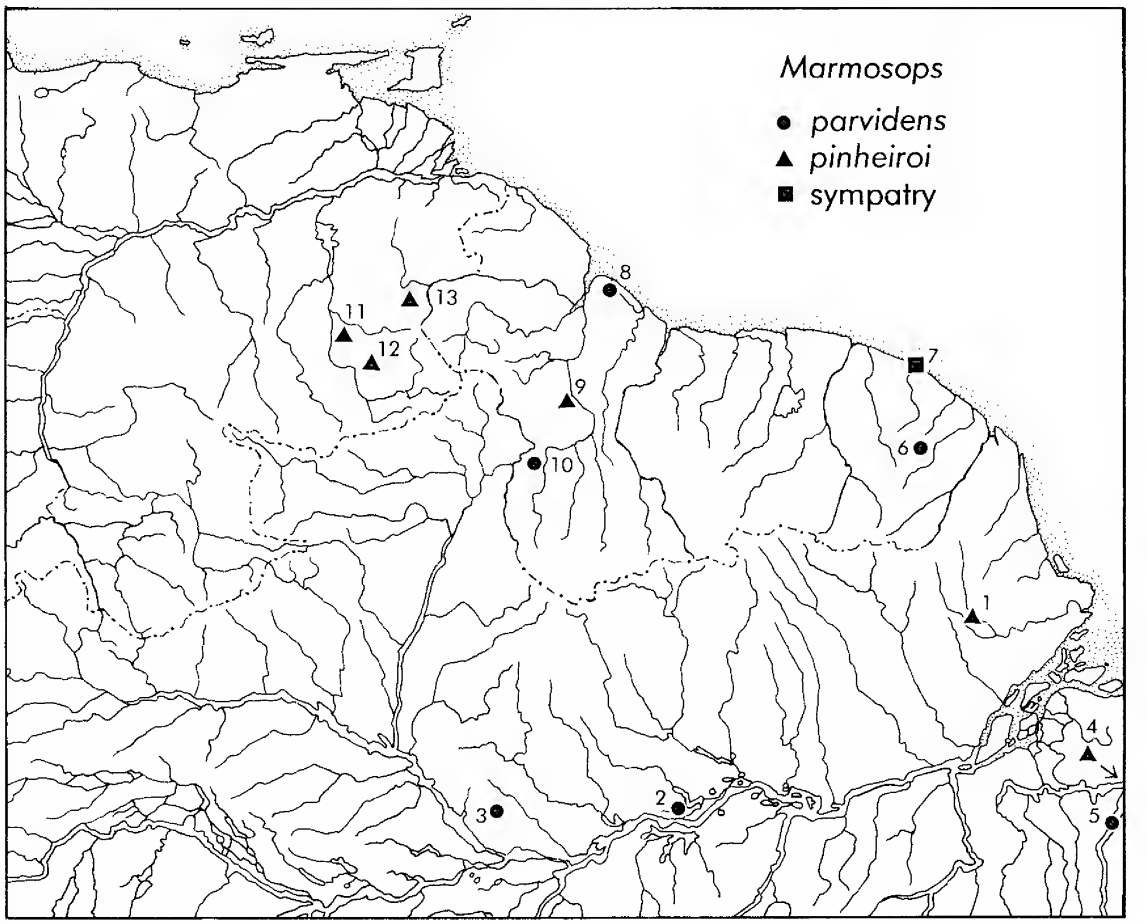

Fig. 27. Known collection localities for *Marmosops parvidens* and *M. pinheiroi* based on specimens examined. **1,** BRAZIL, *Amapá,* Serra do Navio; **2,** BRAZIL, *Amazonas,* Boca Rio Piratucu; **3,** BRAZIL, *Amazonas,* 80 km N Manaus; **4,** BRAZIL, *Pará,* Belém and Utinga; **5,** BRAZIL, *Pará,* Ilha do Taiuna; **6,** FRENCH GUIANA, Arataye; **7,** FRENCH GUIANA, Paracou; **8,** GUYANA, *Demerara-Mahaica,* Hyde Park; **9,** GUYANA, *Potaro-Siparuni,* Iwokrama Reserve; **10,** *Upper Takutu-Upper Essequibo,* Karanambo; **11,** VENEZUELA, *Bolívar,* Auyan-tepui; **12,** VENEZUELA, *Bolívar,* Churi-tepui; **13,** VENEZUELA, *Bolívar,* 85 km SE El Dorado. One collection locality for *Marmosops pinheiroi* (Belém/Utinga, in the Brazilian state of Pará) lies just outside the right margin of this map.

viduals (64%) were shot, sighted, or trapped in well-drained primary forest, but one (4%) was encountered in swampy primary forest, four (18%) in primary forest of unspecified character, and three (14%) in secondary vegetation. With the exception of females with nursing young, all shot, sighted, or trapped animals were solitary.

One female shot on 7 July 1991 had seven nursing young measuring 19 mm crown-rump, and another shot on 17 August 1991 had eight nursing young measuring 29 mm crown-rump.

Micoureus demerarae (Thomas)

VOUCHER MATERIAL: AMNH 266428, 266429, 266431–266434, 267370, 267371, 267818; MNHN 1995.911–1995.914. Total = 13 specimens.

IDENTIFICATION: Although our voucher material corresponds closely to Tate's (1933) and Husson's (1978) descriptions of this taxon, the coloration of the ventral pelage and of the tail are variable among Paracou specimens and merits comment. Most of the ventral surface is covered by gray-based fur that

TABLE 11
Measurements (mm) and Weights (g) of Adult *Metachirus nudicaudatus* from French Guiana

	Paracou vouchers[a]		Holotyped
	Males[b]	Females[c]	
HBL	270 (255–287) 4	256 (249–271) 5	—
LT	345 (335–369) 4	345 (326–370) 5	—
HF	46 (44–49) 4	44 (41–45) 5	—
Ear	38 (37–40) 4	39 (35–41) 5	—
CBL	60.2 (60.0–60.4) 3	57.7 (56.5–59.5) 5	—
LM	11.9 (11.8–12.1) 4	11.9 (11.6–12.2) 5	11.8
PB	17.6 (17.4–18.2) 4	17.4 (16.7–18.3) 5	17.6
PL	34.0 (33.2–34.5) 3	33.1 (32.1–34.1) 5	32.2
LPB	9.8 (9.3–10.0) 3	9.3 (9.0–9.5) 5	10.2
ZB	29.3 (28.7–30.2) 3	26.6 (25.8–27.4) 3	27.1[e]
Wt	432 (360–480) 4	338 (260–410) 5	—

[a] Summary statistics include the sample mean, the observed range (in parentheses), and the sample size.
[b] AMNH 266450, 267009, 267010; MNHN 1995.906.
[c] AMNH 266435, 266440, 266449, 266455; MNHN 1995.907.
[d] MNHN 1990.420, an adult female from Cayenne.
[e] Estimated value.

is heavily washed with buff, but self-colored (pure buff) hairs cover the groin and throat, and a few specimens have narrow streaks of pure buff fur along the midline of the chest or abdomen. The tails of most Paracou specimens have white tips or are mottled with large white spots distally, but two adults (AMNH 267370, 267818) have entirely dark tails.

The holotype (BMNH 5.11.1.25) and other adult specimens from Guyana that we measured for comparison exhibit broad morphometric overlap with our vouchers (table 12). Additionally, fresh Guyanese skins (e.g., ROM 103370, 104708) are indistinguishable in coloration from our Paracou material. Thus, although several valid taxa may eventually be recognized among the many names currently synonymized with *Micoureus demerarae* (see below), the Paracou population can be confidently assigned to this species, and to the nominate race if a trinomial nomenclature is warranted.

Juveniles of *Micoureus demerarae* somewhat resemble *Marmosa murina* in size and external appearance, and the two species might therefore be confused in the field, even with specimens in hand. Based on our material, the best external characters for discrimination are tail color (most, but not all, examples of *M. demerarae* have tails blotched or tipped with white, whereas *M. murina* has consistently all-dark tails), fur texture (longer and woolly in *M. demerarae,* close and smooth in *M. murina*), the extent of fur at the base of the tail (conspicuously greater in *M. demerarae* than in *M. murina*), and size of the manual claws (extending beyond the fleshy apical pads in *M. demerarae* but not in *M. murina*).

REMARKS: Originally described as a subspecies of *Marmosa cinerea* by Thomas (1905), *demerarae* was treated as a distinct species of the *cinerea* group in Tate's (1933) monographic revision of *Marmosa* (sensu lato). Cabrera (1958), however, considered *demerarae* to be a subspecies of *cinerea,* citing doubts that Tate (1939: 164, footnote 2) expressed about his own prior classification. The current allocation of Tate's *cinerea* group to *Micoureus* follows Gardner and Creighton (1989). Among the many nominal taxa now synonymized with *Micoureus demerarae* (sensu Gardner, 1993) are several that Tate (1933) recognized as full species, all or some of which may yet prove to be valid (Patton et al., 2000). With the extensive series of specimens now available to evaluate the taxonomy of this widespread complex, the group is ripe for modern revisionary treatment.

OTHER SPECIMENS EXAMINED: **Guyana**—"R. Demerara" (BMNH 7.6.20.14); *Cuyuni-Mazaruni,* Kartabo (AMNH 42887, 64156); *Potaro-Siparuni,* 5 km SE Surama (ROM 103146), Iwokrama Reserve (ROM 104708); *Upper Demerara-Berbice,* Comackka on Demerara River (BMNH 5.11.1.25 [holotype]), Tropenbos (ROM 103370); *Upper Takutu-Upper Essequibo,* Achamere Wan (ROM 34514), Ireng Valley (BMNH 3.4.6.10), Kuitaro River 40 mi E Dadanawa (ROM 35453), Weri More (ROM 33201).

FIELD OBSERVATIONS: All of our definite records of *Micoureus demerarae* at Paracou are based on collected specimens; of these, eight were shot, three were caught in Victor traps, and two were caught in elevated platform traps. Most (12) of our specimens were taken 1–17 m above the ground on lianas or in trees, but one juvenile was found climbing

TABLE 12
Measurements (mm) and Weights (g) of Adult *Micoureus demerarae*

	Paracou vouchers			Other Guyanese specimens	
	Males[a]	Female[b]	Type[c]	Males[d]	Females[e]
HBL	180 (170–193) 6	172	166[f]	169 (157–181) 2	174 (165–184) 2
LT	261 (253–280) 6	238	250[f]	256 (245–267) 2	237 (234–240) 2
HF	28 (27–29) 6	26	27[g]	28 (27–29) 2	24 (24–25) 2
Ear	29 (27–31) 6	28	—	30 (29–30) 2	28 (26–31) 2
CBL	43.6 (42.1–44.5) 5	41.1	40.0	43.2 (40.6–45.3) 4	40.8 (38.9–44.1) 5
LM	8.6 (8.3–8.7) 6	8.3	8.4	8.6 (8.3–8.9) 4	8.4 (8.3–8.5) 6
PB	14.0 (13.4–14.6) 6	13.4	13.2	14.0 (13.2–14.3) 4	13.3 (13.0–13.8) 5
PL	24.2 (23.2–25.1) 6	22.5	22.0	23.8 (22.2–24.7) 4	22.8 (22.2–24.1) 5
LIB	7.7 (7.2–8.2) 6	—	7.0	7.6 (6.9–8.1) 4	7.1 (6.6–7.7) 6
ZB	24.7 (24.1–25.4) 5	23.1	23.1	24.9 (23.1–26.7) 3	23.1 (21.5–24.6) 5
Wt	115 (93–149) 6	89	—	102 (94–110) 2	98 (98) 1

[a] The mean, the observed range (in parentheses), and the sample size are provided for the following series of specimens: AMNH 266428, 266431, 267370, 267371, 267818; MNHN 1995.912.
[b] AMNH 266432.
[c] BMNH 5.11.1.25, female.
[d] AMNH 42887; BMNH 7.6.20.14; ROM 103146, 104708.
[e] AMNH 64156; BMNH 3.4.6.10; ROM 33201, 34514, 35453, 103370.
[f] Measurement from Thomas (1905).
[g] Measurement from Tate (1933: table I).

among dead branches at ground level in a treefall. Five specimens were collected in well-drained primary forest, one in swampy primary forest, and seven in more-or-less disturbed habitats (roadside secondary growth and selectively logged forest).

Our single adult female specimen, collected on 12 August, was not carrying suckling young.

Monodelphis brevicaudata (Erxleben)

Figures 29–31

VOUCHER MATERIAL: AMNH 267000. Total = 1 specimen.

IDENTIFICATION: The genus *Monodelphis* has never been revised, and many aspects of the currently accepted species-level taxonomy of these short-tailed opossums (summarized by Gardner, 1993) remain untested by substantive analyses of specimen data. To determine the correct identification of our single Paracou voucher, we examined comparative series, types, and original descriptions of all relevant taxa. Our resulting systematic conclusions broadly overlapped those of the late C. O. Handley, Jr., who generously shared with us the unpublished results of his previous research with many of the same specimens that we studied. His suggestions prompted us to reexamine some of our earlier ideas about character variation in the *M. brevicaudata* complex, and the following account therefore reflects his critical input.

Among the many named forms of red-flanked *Monodelphis* currently synonymized with *M. brevicaudata* (see Gardner, 1993) are several readily diagnosable taxa that we provisionally recognize as full species. As understood by us, *M. brevicaudata* is restricted to the Guiana subregion of Amazonia (fig. 28) and is distinguished from other species of the *brevicaudata* complex, all of which are allopatric, by the extension of body fur onto the proximal one-third or more of the caudal dorsum; the ventral surface of the tail is just furred at the base (fig. 29). By contrast, only the basal one-sixth or less of the tail is furred, to about the same extent above and below, in *M. palliolata* (which occurs west of the Orinoco in northern Venezuela and northeastern Colombia), *M. glirina* (south of the Amazon and west of the Xingu), and in an unnamed form (a subspecies of *M. brevicaudata* in the view of C. O. Han-

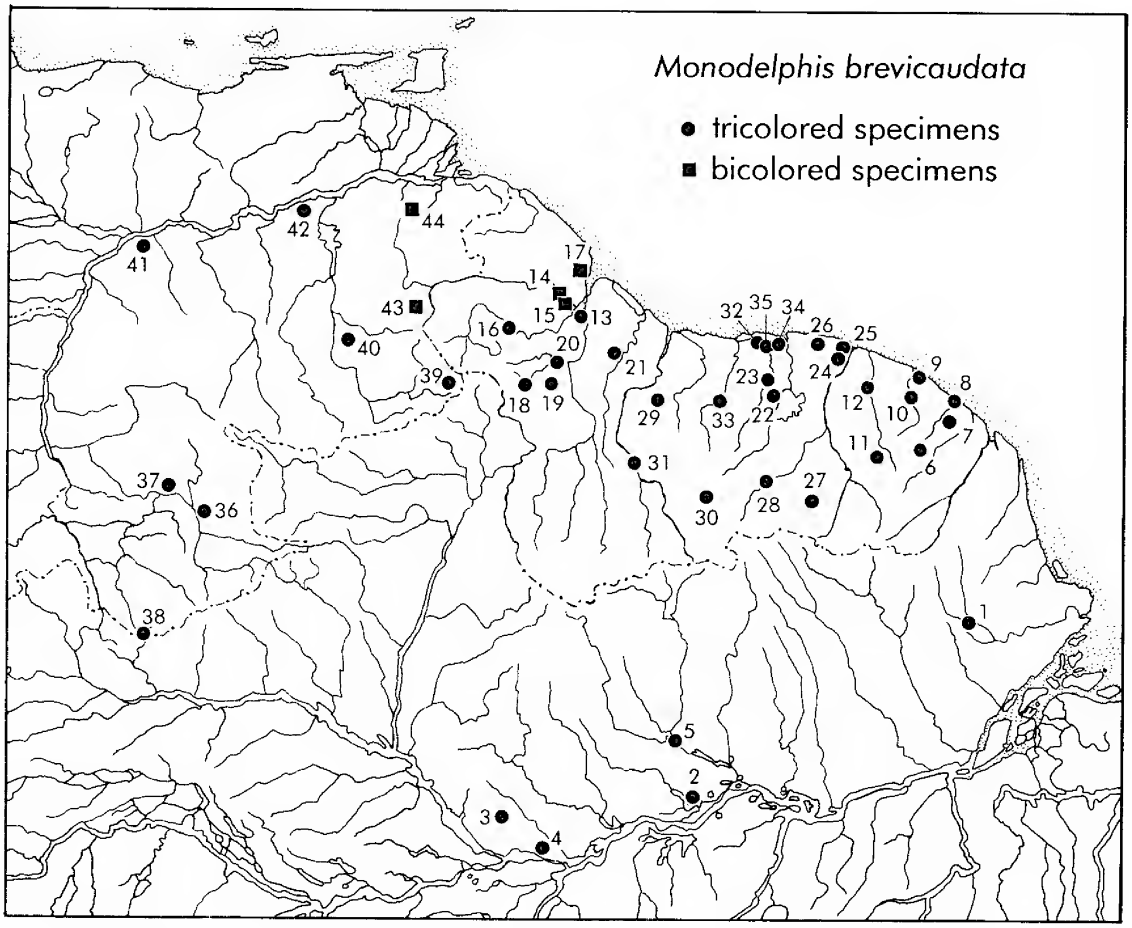

Fig. 28. Known collection localities for *Monodelphis brevicaudata* based on specimens examined. **1,** BRAZIL, *Amapá,* Serra do Navio; **2,** BRAZIL, *Amazonas,* Faro; **3,** BRAZIL, *Amazonas,* 80 km N Manaus; **4,** BRAZIL, *Amazonas,* Sto. Antonio de Amatary; **5,** BRAZIL, *Pará,* Cachoeira Porteira; **6,** FRENCH GUIANA, Arataye; **7,** FRENCH GUIANA, Cacao; **8,** FRENCH GUIANA, Cayenne and Montjoly; **9,** FRENCH GUIANA, Paracou; **10,** FRENCH GUIANA, St.-Eugène; **11,** FRENCH GUIANA, Sophie; **12,** FRENCH GUIANA, Tamanoir; **13,** GUYANA, *Cuyuni-Mazaruni,* Bartica Grove; **14,** GUYANA, *Cuyuni-Mazaruni,* First Falls on Cuyuni River; **15,** GUYANA, *Cuyuni-Mazaruni,* Kartabo; **16,** GUYANA, *Cuyuni-Mazaruni,* Kamakusa; **17,** GUYANA, *Essequibo Islands-West Demerara,* Buck Hall; **18,** GUYANA, *Potaro-Siparuni,* Anundabaru; **19,** GUYANA, *Potaro-Siparuni,* Minnehaha Creek; **20,** GUYANA, *Potaro-Siparuni,* Potaro; **21,** GUYANA, *Upper Demerara-Berbice,* Dubulay Ranch; **22,** SURINAM, *Brokopondo,* Brownsberg; **23,** SURINAM, *Brokopondo,* Finisanti; **24,** SURINAM, *Marowijne,* Albina; **25,** SURINAM, *Marowijne,* Langamankondre; **26,** SURINAM, *Marowijne,* 10 km N and 24 km W Moengo; **27,** SURINAM, *Marowijne,* Oelemarie; **28,** SURINAM, *Marowijne,* Paloemeu Airstrip; **29,** SURINAM, *Nickerie,* Avanavero; **30,** SURINAM, *Nickerie,* Kayserberg Airstrip; **31,** SURINAM, *Nickerie,* King Frederick William Falls; **32,** SURINAM, *Saramacca,* La Poule; **33,** SURINAM, *Saramacca,* Raleigh Falls; **34,** SURINAM, *Suriname,* Paramaribo; **35,** SURINAM, *Suriname,* Jarikaba near Uitkijk; **36,** VENEZUELA, *Amazonas,* Boca Rio Ocamo; **37,** *Amazonas,* Esmeralda and Mt. Duida; **38,** VENEZUELA, *Amazonas,* Serra de Neblina; **39,** VENEZUELA, *Bolívar,* Arabupu; **40,** VENEZUELA, *Bolívar,* Auyantepui; **41,** VENEZUELA, *Bolívar,* Caicara; **42,** VENEZUELA, *Bolívar,* Ciudad Bolívar; **43,** VENEZUELA, *Bolívar,* 65 km SSE El Dorado; **44,** VENEZUELA, *Bolívar,* Reserva Forestal Imataca.

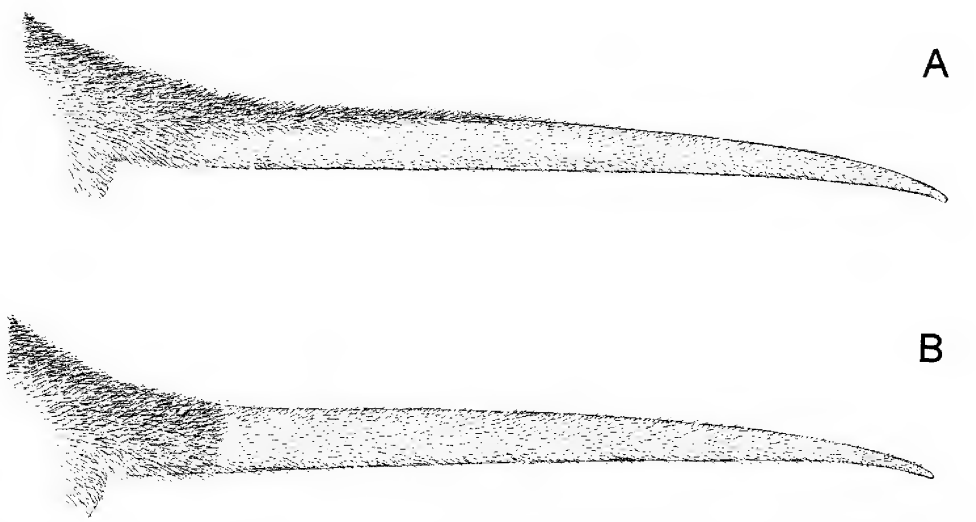

Fig. 29. Distribution of body pelage on tails of *Monodelphis brevicaudata* (**A,** AMNH 93972) and *M. palliolata* (**B,** AMNH 69942). In *brevicaudata,* body fur extends onto the caudal dorsum for one-third or more of the length of the tail, but the caudal ventrum is only furred at the base. In *palliolata* and other taxa formerly synonymized with *brevicaudata,* the base of the tail is furred to about the same extent above and below. Both views about ×1.2.

dley, Jr., personal commun.) distributed south of the Amazon and east of the Xingu. In addition, whereas *M. palliolata* and *M. glirina* have orange ventral fur (not sharply differentiated from the color of the flanks) and a broad cap of grizzled-grayish fur extending across the crown of the head between the eyes, fully adult specimens of *M. brevicaudata* have whitish, cream, or buffy ventral fur (sharply differentiated from the reddish flanks) and a narrower cap of grizzled-grayish fur that (when present) is confined middorsally by a broad band of red above each eye. *Monodelphis palliolata* and *M. glirina* are externally similar, but differ in size (upper molar row ≤7.9 mm in *palliolata,* ≤7.9 mm in *glirina*). The unnamed form south of the Amazon and east of the Xingu resembles geographically adjacent populations of *M. brevicaudata* (from Amapá and the eastern Guianas) in size and coloration but lacks the dorsal extension of body fur onto the tail.

Thus restricted, *Monodelphis brevicaudata* includes the following nominal taxa: *brevicaudata* Erxleben (1777), *brachyuros* Schreber (1778), *touan* Shaw (1800), *tricolor* Geoffroy (1803), *hunteri* Waterhouse (1841), *orinoci* Thomas (1899b), and *dorsalis* Allen (1904). The material we examined exhibits considerable geographic variation in pelage color, the taxonomic significance of which is difficult to evaluate. Possibly, pelage color may reflect species-level divergence that is not apparent in craniodental characters, but the material currently available is insufficient to determine whether chromatic variation is clinal or discontinuous. The following observations are intended to establish which of the above names is applicable to the coat-color phenotype represented by our Paracou voucher, not to revise the nomenclature of the entire *brevicaudata* complex, a task beyond the scope of this report.

Erxleben's (1777) description of *Didelphis brevicaudata* and Schreber's (1778) description of *Didelphys brachyuros* were both based on Seba's (1734: 50) description and illustration (op. cit.: pl. xxxi, fig. 6) of "*Muris sylvestris Americani faemina*". Seba's original specimen (BMNH 67.4.12.540; see Thomas, 1892) is therefore the type of both *brevicaudata* and *brachyuros,* so these nominal taxa are objective synonyms (for the priority of Erxleben's name see Thomas, 1888: 356). We examined BMNH 67.4.12.540, an adult female preserved in fluid with an extracted skull. Despite more than two centuries in preservative, this specimen is in re-

markably good condition and the apparently unfaded pelage is distinctly bicolored (reddish dorsally and abruptly paler ventrally), exactly as described by Seba, Erxleben, and Schreber; there is no middorsal stripe of grizzled-brownish, -grayish, or -blackish fur. Although Matschie (1916) restricted the type locality of *Monodelphis brevicaudata* to Surinam, bicolored specimens resembling the type are only known from the interfluvial region between the lower Caroni-Orinoco and the lower Mazaruni-Essequibo in northeastern Venezuela and northwestern Guyana (fig. 28). Because Matschie's restriction was obviously erroneous, we hereby emend the type locality to the vicinity of Kartabo, Cuyuni-Mazaruni District, Guyana (locality 15 in fig. 28), from which a well-preserved bicolored specimen (AMNH 48133) closely resembling the type was collected by William Beebe in 1919.[8]

By contrast with the limited geographic distribution of bicolored animals, tricolored specimens of *Monodelphis brevicaudata* have been collected throughout French Guiana, Surinam, Guyana, Guianan Venezuela (south and east of the Orinoco), and Guianan Brazil (north of the Amazon and east of the Rio Negro). In fully adult examples of this coat-color phenotype, a broad middorsal stripe of grizzled-brownish, -grayish, or -blackish fur is sharply set off from the clear (ungrizzled) reddish flanks, which are separated by a similarly abrupt transition from the pale (whitish, cream, or buffy, but sometimes partly gray-based) ventral fur. Whereas tricolored skins from Brazil and the Guianas are often brightly colored (with blackish or grayish middorsal stripes and cream or whitish venters), most tricolored Venezuelan skins have brownish middorsal stripes and buffy venters that exhibit less chromatic contrast with the reddish flanks. Despite Husson's (1978) remark that his Surinamese specimens represented a full range of intermediates between the bicolored and tricolored phenotypes, all of the Surinamese specimens we examined (including Husson's material, obtained on loan from the RMNH) are tricolored.

The oldest available name for any tricolored form of *Monodelphis brevicaudata* is *Viverra touan* Shaw (1800), which was based on Buffon's (1789) description of "Le Touan" from Cayenne.[9] That the name *touan* properly applies to the tricolored phenotype is unambiguously supported both by Buffon's and Shaw's explicit mention of a blackish middorsal stripe extending from the rostrum to the base of the tail, and by the fact that only tricolored animals are known from French Guiana. The appropriate trinomial, if one is needed, for our Paracou voucher is therefore *M. b. touan.* Unfortunately, the application of the name *touan* has been a persistent source of confusion in the literature. Thomas (1888) and Cabrera (1919) regarded *touan* as a synonym of *brevicaudata,* but Cabrera (1958) listed *touan* (without comment) as a distinct species that included such divergent forms as *emiliae, paulensis,* and *rubida* as subspecies. Current usage (Gardner, 1993) recognizes *M. emiliae, M. rubida,* and *M. sorex* (including *paulensis*) as full species that can be distinguished from *M. brevicaudata* by trenchant craniodental characters (e.g., those described by Pine and Handley, 1984).

In a recent treatment of Venezuelan *Monodelphis,* Linares (1998) inexplicably reversed the application of *touan* and *brevicaudata* by assigning the former name to the bicolored phenotype and the latter name to tricolored animals (including *M. palliolata*). According to Linares, *touan* and *brevicaudata* are distinguished by craniodental characters in addition to pelage color pattern, and occur sympatrically in northeastern Venezuela, the Guianas, and in the Brazilian state of Pará. However, specimens referable to *touan* and *brevicaudata* are not craniodentally dif-

[8] Kyk-over-al, a small island opposite Kartabo at the confluence of the Cuyuni and Mazaruni Rivers, was the seat of government of the Dutch colony of Essequibo from the early 1600s until 1740 (Beebe, 1925). The environs of Kartabo (Kartabu Point on recent maps; 6°23′N, 58°41′W) are therefore a plausible source of some of the South American material assembled by Albert Seba (b.1665, d.1736; Engel, 1937) in Amsterdam.

[9] *Didelphis tricolor* E. Geoffroy is another name proposed for "Le Touan", but it is based on a different specimen in the Paris museum than that illustrated and described by Buffon (Geoffroy, 1803). The type of *tricolor* (MNHN 1990.421), like Buffon's lost specimen, was apparently collected by M. de la Borde of Cayenne (Julien-Laferrière, 1994).

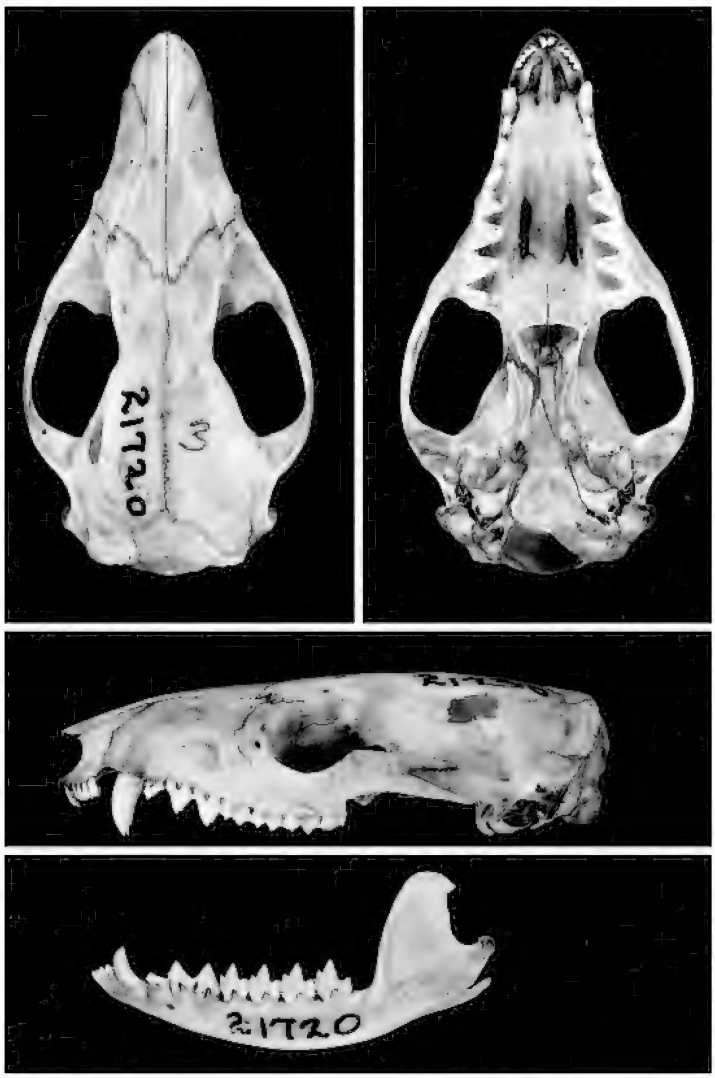

Fig. 30. Dorsal, ventral, and lateral cranial views of FMNH 21720, neotype of *Viverra touan* Shaw (= *Monodelphis brevicaudata*). All views approximately ×2.

ferentiated in our experience, nor have we seen evidence that two species assignable to the *brevicaudata* complex are sympatric anywhere. Linares also resurrected Cabrera's (1958) hypothesis that *touan* and *emiliae* are conspecific, but our observations support Pine and Handley's (1984) conclusion that *emiliae* is a distinctive species with no special similarity to *touan* or to other members of the *brevicaudata* complex.

In order to definitively resolve these conflicting usages, we hereby designate FMNH 21720 as the neotype of *Viverra touan* Shaw. The neotype, consisting of the skull (fig. 30) and the tricolored skin (fig. 31) of an adult male, was collected by S. Klages at Cayenne, French Guiana, on 26 February 1917.

Despite the conspicuous geographic variation in pelage color within *Monodelphis brevicaudata* noted above, we are not persuaded of the necessity for a formal trinomial nomenclature. Although the *brevicaudata* and *touan* phenotypes are clearly distinct in Guyana, some bicolored Venezuelan specimens from NE Bolívar (e.g., EBRG 17536, USNM 385004, 385005) have indistinctly

Fig. 31. Dorsal, lateral, and ventral views of the skin of FMNH 21720, neotype of *Viverra touan* Shaw (= *Monodelphis brevicaudata*). All views approximately life-size.

grizzled middorsal fur, somewhat resembling the middorsal pigmentation of drab-tricolor skins from Amazonas and southeastern Bolívar, an observation that could be interpreted as evidence that bicolored and tricolored populations intergrade clinally in Guianan Venezuela. Furthermore, although our samples of measurable adults are too small for

TABLE 13
Measurements (mm) of Adult *Monodelphis brevicaudata*[a]

	Tricolored specimens from French Guiana[b]				
	Paracou voucher[c]	Other material		Bicolored specimens[f]	
		Males[d]	Females[e]	Males[g]	Females[h]
HBL	—	136 (111–157) 4	139 (135–141) 3	158 (140–170) 3	161 (161–161) 1
LT	—	76 (71–80) 4	77 (69–86) 3	87 (85–89) 2	76 (76–76) 1
HF	—	22 (20–25) 5	21 (21–22) 3	23 (22–23) 4	23 (22–23) 3
Ear	—	19 (18–19) 3	17 (16–18) 3	20 (19–22) 2	20 (20–20) 1
CBL	37.1	38.9 (35.2–44.3) 5	35.0 (35.0–35.0) 2	38.3 (36.9–39.8) 2	36.8 (36.7–36.9) 2
LM	8.2	7.9 (7.5–8.1) 5	7.8 (7.4–8.2) 3	8.0 (7.8–8.3) 4	7.6 (7.2–8.0) 3
PB	12.4	12.5 (11.8–13.1) 5	11.7 (11.4–12.0) 3	12.5 (12.0–12.8) 3	11.5 (11.1–11.8) 3
PL	20.2	21.6 (19.8–24.4) 5	19.1 (18.9–19.3) 3	21.5 (20.0–22.8) 3	19.8 (18.5–20.4) 3
LPB	6.3	6.1 (6.0–6.2) 5	5.9 (5.7–6.3) 3	6.2 (5.9–6.4) 3	5.8 (5.4–6.1) 3
ZB	19.9	20.8 (19.3–23.0) 5	18.2 (18.2–18.3) 3	21.3 (20.2–22.3) 2	19.4 (19.2–19.6) 2

[a] Only one weight datum (a 50-g adult female from French Guiana) is available from any specimen represented in this table. Tabulated sample statistics include the mean, the observed range (in parentheses), and the sample size.

[b] Typical examples of the "*touan*" coat-color phenotype.

[c] AMNH 267000, a partially eaten carcass of unknown sex.

[d] FMNH 21720 (neotype of *touan*), 21793; MNHN 1981.168, 1981.415, 1995.205.

[e] MNHN 1966.2, 1995.3216; USNM 578009.

[f] Typical examples of the "*brevicaudata*" coat-color phenotype. All specimens accompanied by locality data are from NW Guyana or NE Venezuela (see text).

[g] AMNH 48133; BMNH 17.7.7.1, 34.6.30.65; USNM 385004.

[h] BMNH 67.4.12.540 (holotype of *brevicaudata*), 88.1.31.1 (holotype of *hunteri*); USNM 385005.

confident statistical inference (table 13), no morphometric differences are apparent between bicolored and tricolored animals to suggest that these are anything more than local coat-color variants. Larger series of specimens, especially from western Guyana and eastern Venezuela, together with molecular data would be helpful in any future effort to evaluate the taxonomic significance of pelage color variation in this species.

BICOLORED SPECIMENS EXAMINED: **Guyana**—*Cuyuni-Mazaruni,* First Falls on the Cuyuni River (BMNH 34.6.30.65), Kartabo (AMNH 48133); *Essequibo Islands-West Demerara,* Buck Hall (BMNH 17.7.7.1). **Venezuela**—*Bolívar,* 65 km SSE El Dorado (USNM 385005), 56 km SE El Manteco (USNM 385004), Reserva Forestal Imataca (EBRG 17536). **Without locality data**—(BMNH 67.4.12.540 [holotype of *brevicaudata*], 88.1.31.1 [holotype of *hunteri*]).

TRICOLORED SPECIMENS EXAMINED: **Brazil**—*Amapá,* Serra do Navio (USNM 392050, 392051, 393424, 393428, 393430, 393435, 393436, 393438, 393439, 393441, 461434, 461435); *Amazonas,* Faro (AMNH 93972–93974, 94161, 94221), 80 km N Manaus (USNM 579976–579979), Santo Antonio da Amatary (AMNH 92879); *Pará,* Cachoeira Porteira (USNM 546209–546219), "Serra do Tumucumaque" (USNM 392044–392049). **French Guiana**—Arataye (USNM 578009), Cacao (MNHN 1981.168, 1981.412, 1981.414–1981.416, 1982.599), Cayenne (FMNH 21720 [neotype of *touan*], MNHN 1990.421 [holotype of *tricolor*]), Montjoly (MNHN 1994.122), St.-Eugène (MNHN 1995.205, 1995.3216), Sophie (MNHN 1966.1, 1966.2), Tamanoir (FMNH 21793), Trois Sauts (MNHN 1981.413). **Guyana**—"River Supinaam" (BMNH 10.9.29.26, 10.9.29.27); *Cuyuni-Mazaruni,* Bartica Grove (BMNH 10.11.10.20), Kamakusa (AMNH 140465, 140466); *Potaro-Siparuni,* Anundabaru (AMNH 75830, 75831), Minnehaha Creek (AMNH 36317), Potaro (BMNH 12.6.9.9); *Upper Demerara-Berbice,* Dubulay Ranch (AMNH 267744, 268060, 268061). **Surinam**—*Brokopondo,* Brownsberg (CM 52729, RMNH 23403, 23404), Finisanti (FMNH 95338); *Marowijne,* 3 km SW Albina (CM 76730), Langa-

Fig. 32. Capture site of *Monodelphis brevicaudata* at Paracou. Our single voucher specimen was trapped in the dark cave-like space (white arrow) beneath this fallen tree in well-drained primary forest. Such cavities, carpeted and sheltered by decaying wood, are typical microhabitats for *Monodelphis* species but not for other Neotropical rainforest marsupials. All of the other nonvolant mammals captured under fallen trees at Paracou were rodents, including *Neacomys paracou, Oryzomys megacephalus, O. yunganus,* and *Proechimys cuvieri.*

mankondre (RMNH 18227), 10 km N and 24 km W Moengo (CM 52730), Oelemarie (CM 76731, 76732), Paloemeu Airstrip (FMNH 94018, 94019); *Nickerie,* Avanavero (CM 68358), Kayserberg Airstrip (CM 68359), King Frederick William Falls (FMNH 48416); *Saramacca,* La Poule (FMNH 95339), Raleigh Falls (CM 63510, 63511, 68361); *Suriname,* Cultuurtuin near Paramaribo (RMNH 18076), Jarikaba near Uitkijk (RMNH 20672), Plantage De Morgenstond near Paramaribo (RMNH 17223), Plantation Clevia near Paramaribo (RMNH 21654). **Venezuela**—*Amazonas,* Boca Río Ocamo (AMNH 78093–78095), Esmeralda (AMNH 77281, 77282, 77287, 77288), Mt. Duida (AMNH 77283–77285, 77289, 77290–77296), "Río Casiquiare" (AMNH 77286, 78096–78100), Serra de Neblina (AMNH 244469); *Bolívar,* Arabupu (AMNH 75681–75687), Auyantepui (AMNH 130516, 130560–130565, 130573–130576, 130727), Caicara (BMNH 98.12.1.22 [holotype of *orinoci*]), Ciudad Bolívar (AMNH 16124–16126 [type series of *dorsalis*].

FIELD OBSERVATIONS: The single example of *Monodelphis brevicaudata* that we collected at Paracou is a partially eaten specimen caught in a Victor trap set under a fallen tree (fig. 32) in well-drained primary forest. Several additional specimens were previously taken by O. Henry in the course of his multiyear trapping study (G. Dubost, personal commun.), but we have not examined his material.

Philander opossum (Linnaeus)

VOUCHER MATERIAL: AMNH 266379–266381, 266383–266387, 266389–266391,

TABLE 14
Measurements (mm) and Weights (g) of Adult *Philander opossum* from French Guiana and Surinam[a]

	Paracou vouchers		Surinamese specimens[b]	
	Males[c]	Females[d]	Males[e]	Females[f]
HBL	310 (293–323) 3	298 (264–346) 8	285 (264–305) 3	292 (255–325) 8
LT	318 (302–333) 3	302 (280–317) 8	272 (255–281) 3	308 (280–332) 8
HF	45 (43–46) 3	43 (41–44) 8	43 (42–44) 3	43 (41–46) 8
Ear	40 (38–43) 3	39 (36–42) 8	38 (35–39) 3	40 (37-45) 8
CBL	78.7 (77.4–79.7) 3	72.2 (67.1–78.6) 8	72.4 (72.0–72.8) 3	72.5 (67.7–75.8) 8
LM	14.7 (14.6–14.8) 3	14.4 (13.6–15.4) 8	13.8 (13.6–14.0) 2	13.9 (13.1–14.2) 8
PB	21.1 (20.8–21.5) 3	21.0 (19.9–21.9) 8	20.1 (19.9–20.3) 3	20.4 (19.8–21.2) 8
PL	46.2 (45.6–46.6) 3	43.2 (40.2–46.9) 8	43.1 (42.6–44.1) 3	43.4 (41.1–45.6) 8
LIB	13.9 (13.7–14.3) 3	12.1 (11.5–12.9) 5	13.5 (12.2–14.5) 3	12.6 (11.8–13.3) 8
ZB	39.8 (37.6–41.6) 3	35.5 (33.0–39.3) 8	37.7 (34.9–39.3) 3	35.9 (32.3–38.2) 8
Wt	678 (660–695) 2	501 (380–680) 8	495 (340–650) 2	470 (280–585) 8

[a] Summary statistics include the sample mean, the observed range (in parentheses), and the sample size.
[b] Measured specimens were collected within 100 km of Paramaribo.
[c] AMNH 266379, 266381, 267014.
[d] AMNH 266383, 266386, 266387, 266995, 267328; MNHN 1995.917–1995.919.
[e] CM 76744; FMNH 95309, 95310.
[f] CM 52734, 52735, 52741, 52742, 68365, 76736, 76742, 76743.

266394, 266395, 266398, 266400, 266994, 266995, 266997–266999, 267014, 267328; MNHN 1995.915–1995.924. Total = 32 specimens.

IDENTIFICATION: The species-level taxonomy of *Philander* was recently reviewed by Hershkovitz (1997) and by Patton and da Silva (1997), whose taxonomic conclusions differ considerably. Both studies, however, referred Guianan populations of gray four-eyed opossums to *P. opossum,* the type locality of which (as restricted by Matschie, 1916) is Paramaribo, Surinam. Our Paracou vouchers agree closely with Husson's (1978) description of topotypic specimens of *P. opossum* in most details, but a few discrepancies merit comment. (1) Whereas Husson described the pelage of his topotypes as usually distinctly darker middorsally than on the sides, only one skin from Paracou (AMNH 266995) has fur that is slightly darker middorsally than on the sides; the rest of the adult and subadult skins from Paracou are a uniform grizzled-gray over the entire dorsum. (2) Husson (1978: 25) described the fur of the head as "of the same dark blackish-brown colour as the median part of the back or even slightly darker", but the blackish fur of the head contrasts conspicuously with the grizzled-gray back in all adult and subadult Paracou skins, even the aforementioned example with darker middorsal fur. (3) Husson (1978: 26) described the ears as "whitish with a broad black rim", but the ears of our Paracou specimens are only whitish at the base—most of the pinna is black. (4) Husson's juvenile specimens were described as darker than adults and with less distinct facial markings, but three juvenile skins from Paracou (AMNH 266385, 266391, 266997) are comparable to those of adults and subadults except in pelage texture (the juvenile fur is softer).

Although most of the Surinamese material we borrowed for side-by-side comparison are darker middorsally than on the sides, as Husson described, a few (e.g., CM 52735) are uniformly gray like our Paracou vouchers. The other external differences implied by Husson's description are not apparent in the Surinamese material we examined.[10] Cranial measurements of adult females from Paracou

[10] Some color variation among the series at hand may be artifactual. For example, the blackish color of the crown of the head probably fades with age (becoming dusky-brown on old skins), and dark-tipped dorsal hairs may be more concentrated in the midline of flat skins than on round skins.

and Surinam overlap broadly (table 14), but our few adult males seem exceptionally large. We did not see any consistent qualitative craniodental differences between Surinamese and Paracou specimens.

Patton and da Silva (1997: 98) characterized the phenotype of *Philander opossum* as "uniformly pale-gray", a description that better fits our Paracou material than it does the Surinamese topotypes we examined. However, Patton and da Silva's context for taxonomic comparisons included the almost entirely black *P. mcilhennyi,* as well as the black-striped *P. andersoni,* both of which contrast strikingly with predominantly grayish animals that those authors referred to *P. opossum* and *P. frenata.*

According to Hershkovitz (1997: 39), both gray and "brown" color phases occur throughout the range of *P. opossum.* We examined the Surinamese specimens that he cited as coat-color exemplars, however, and did not observe any consistent differences between gray and "brown" individuals (e.g., between FMNH 95312 and 95313, both collected by H. A. Beatty in the Wilhelmina Mountains). Yellowish or brownish tints do occur in some *Philander* skins, but whether these represent true coat-color variants rather than preservational artifacts (e.g., staining by sebaceous secretions or subcutaneous fat) is difficult to determine with the material at hand.

Both Patton and da Silva (1997) and Hershkovitz (1997) referred French Guianan populations of *Philander opossum* to the nominate form *P. o. opossum,* a usage consistent with the results of our comparisons. According to these authors, the nominate race occurs throughout the Guianas and the eastern Amazon basin of Brazil, and differs from other subspecies principally by geographic variation in size and pelage color. However, whereas Patton and da Silva recognized four species of *Philander* (see above), Hershkovitz recognized only *P. opossum* (including *frenata* among other subspecies) and *P. andersoni* (including *mcilhennyi* as a subspecies). We follow Patton and da Silva in recognizing the gray four-eyed opossum of the Brazilian Atlantic forest as a distinct species, *P. frenata,* and we interpret their phylogenetic analysis of mtDNA sequences as evidence that additional taxa currently treated as subspecies of *P. opossum* (e.g., *canus* and *fuscogriseus*) might also be recognized as full species. However, many nominal taxa were not represented in Patton and da Silva's molecular analyses, and several important issues of species-level synonymy remain unresolved. Therefore, the geographic limits of *P. opossum* are still uncertain.

REMARKS: We agree with Hershkovitz (1976, 1981) that *Philander,* not *Metachirops,* is the correct name for pouched four-eyed opossums (contra Husson [1978] and other authors). Linnaeus's (1758) original description of *Didelphis opossum* was based on an adult male and an adult female described and figured by Seba (1734). Hershkovitz (1976: 297) designated Seba's female as the lectotype, but the specimen itself was apparently not then known to have survived the breakup and dispersion of Seba's museum (for the history of which, see Boeseman, 1970). Hershkovitz (1997) subsequently stated that the lectotype is still preserved as an alcoholic specimen in the Rijksmuseum van Naturlijke Historie in Leiden.[11] According to the current RMNH curator of mammals (C. Smeenk, personal commun.), the lectotype is RMNH 25421, clearly recognizable as the adult female with three pouch young illustrated and described by Seba.

OTHER SPECIMENS EXAMINED: **Surinam**—*Coronie,* Totness (CM 52731, 52733); *Marowijne,* Moengo (CM 52734), Perica (CM 76736); *Nickerie,* Avanavero (CM 68363), Kayserberg Airstrip (FMNH 93168), Sipaliwini Airstrip (CM 63517, 76739), Wilhemina Mountains (FMNH 95312, 95313); *Para,* Zanderij (CM 68365, 76742); *Saramacca,* Bigi Poika (CM 52735), La Poule (FMNH 95309); *Suriname,* Clevia (FMNH 95310), Lelydorpplan (FMNH 95308), Plantation Clevia (CM 76743, 76744), Powakka (CM 52741, 52742).

FIELD OBSERVATIONS: In addition to data accompanying our 32 voucher specimens, we recorded 18 unvouchered observations of

[11] Hershkovitz (1997) gave no catalog number for the lectotype, and the caption to his (op. cit.) figure 21 confusingly refers to the "Male and female lectotypes [sic] of *Didelphis opossum* Linnaeus (1758)". The caption is an obvious lapsus that does not affect the validity of his earlier (1976) selection of the female as lectotype. Seba's male specimen is therefore a paralectotype.

Philander opossum at Paracou, for a total of 50 documented records of this species. Of our vouchers, 21 (66%) were shot, 5 (16%) were taken in Conibear traps, 3 (9%) were taken in Sherman live traps, 1 was taken in a Tomahawk wire live trap, and 1 was taken in a Victor snap trap, and 1 was caught by hand. One juvenile captured in a pitfall trap and another taken in a Sherman trap were released. Of all 50 records, 31 (62%) were of individuals shot, trapped, or sighted on the ground, whereas 19 (38%) were of individuals shot, trapped, caught by hand, or sighted in trees (or on other elevated substrates such as inclined trunks, lianas, etc.) from 1.5 to 6 m above the ground. With the exception of females carrying nursing young, all *P. opossum* that we encountered were solitary, and all were collected or sighted at night. Of 49 records accompanied by habitat data, 32 (65%) were of individuals encountered in primary forest, usually near streams or in swamps, but occasionally at well-drained sites; 17 observations (35%), however, were based on individuals encountered in roadside secondary growth or other more-or-less disturbed habitats.

One female, collected on 9 July 1991, had two pouch young measuring 49 mm crown-rump; another, collected on 24 October 1992, had three pouch young measuring 24 mm; and a third, collected on 11 August 1993, had four pouch young measuring 27 mm.

Xenarthra

Nine xenarthran species have been definitely recorded from Paracou and it is unlikely that any others occur locally (see appendix 1). Because most xenarthran species are easily recognized by external characters (Husson, 1978; Emmons, 1990, 1997), we collected few vouchers.

Bradypus tridactylus Linnaeus

Three-toed sloths are possibly common at Paracou, but they are seldom seen and we did not encounter any in the course of our fieldwork. P. Petronelli (personal commun., 1993) estimated that the species is sighted about once or twice a year at Paracou, much less frequently than two-toed sloths (see below).

Choloepus didactylus (Linnaeus)

Voucher Material: AMNH 265952, MNHN 1995.952. Total = 2 specimens.

Identification: Although the species-level taxonomy of two-toed sloths, genus *Choloepus,* has never been formally revised, two species are consistently recognized in modern synoptic treatments of edentate classification (e.g., Wetzel and Ávila-Pires, 1980; Wetzel, 1982, 1985); of these, only *C. didactylus* is known to occur in the Guiana subregion of Amazonia. Our voucher material conforms with the brief description of topotypic specimens of *C. didactylus* from Surinam provided by Husson (1978), and with the cranial diagnosis of this species provided by Wetzel (1985). However, the fur on the throat of our adult female specimen (AMNH 265952) is distinctly paler and shorter than the pectoral fur, a pelage trait that Wetzel regarded as diagnostic of *C. hoffmanni* (from western Amazonia and Central America). The throat fur of our juvenile male (MNHN 1995.952) is likewise paler than the chest fur, but the contrast is less marked than in the adult female. For comparison with Surinamese topotypes measured by Husson (1978: table 38), external measurements of our adult female voucher were 698 × 12 × 164 × 29 mm, and it weighed 7.3 kg. Selected cranial measurements of this specimen are: condylobasal length ("greatest length of skull"), 119.1 mm; zygomatic breadth, 73.0 mm; interorbital constriction, 36.3 mm; alveolar length of maxillary toothrow, 44.5 mm. The ratio of the minimal to the maximal interpterygoid width (after Wetzel, 1985) in this specimen is 0.49.

Field Observations: Two-toed sloths are probably common at Paracou. P. Petronelli (personal commun., 1993) estimated that the species is sighted by forestry workers about five or six times a year in our study area, a reasonably high frequency given its cryptic appearance and inconspicuous habits. Of five sightings by inventory personnel from 1991 to 1994, four were nocturnal and one was diurnal: (1) RSV found a lactating female and a juvenile male (the vouchers described above) hanging together motionless in subcanopy vegetation (ca. 20 m above the ground) in well-drained primary forest at 20:

15 hours on 30 July 1991. (2) RSV found a large adult of undetermined sex descending a tree head-first (probably to defecate) in well-drained primary forest at ca. 23:00 hours on 6 August 1991; the animal was about 2 m above the ground and remained motionless throughout the encounter (about 10 min), even when touched; its eyeshine was very faint. (3) RSV saw another solitary adult of unknown sex sleeping suspended from a liana ca. 4 m above the ground in old secondary growth at 02:00 hours on 31 July 1993. (4) L. H. Emmons saw a solitary animal of unknown sex climbing rapidly about 20 m above the ground in well-drained primary forest at 10:15 hours on 24 September 1994. (5) L. H. Emmons found an adult of unknown sex hanging motionless under a branch about 20 m above a stream in primary forest at 20:21 hours on 5 October 1994.

Cabassous unicinctus (Linnaeus)

The only record of this elusive armadillo at Paracou is an infant specimen (with unopened eyes) excavated by a bulldozer when a tract of well-drained primary forest was being cleared for a new experimental plantation; forestry workers brought the animal to P. Petronelli (personal commun., 1993), who showed us the photographs he had taken of it.

Dasypus kappleri Krauss

VOUCHER MATERIAL: AMNH 267011. Total = 1 specimen.

IDENTIFICATION: Our single voucher conforms exactly in qualitative external and cranial characters to Husson's (1978) and Wetzel and Mondolfi's (1979) descriptions of this species, the type locality of which is in Surinam. For comparison with quantitative data summarized by those authors, the external measurements of our adult male voucher were 565 × 405 × 125 × 53 mm, and it weighed 10.6 kg. The carapace of this specimen has eight movable bands, of which the fourth has 58 scutes; the condylonasal length of the skull is 128.6 mm, the zygomatic width 53.2 mm, and the mastoidal width 35.3 mm; there are eight paired maxillary teeth and eight paired mandibular teeth (meristic counts and cranial measurements follow Wetzel and Mondolfi's conventions).

FIELD OBSERVATIONS: Our single voucher of *Dasypus kappleri* and two other individuals (unambiguously identified but not collected) were all encountered at night, foraging singly on the ground in primary forest. Several other armadillo encounters recorded in our fieldnotes might have been of this species, but positive identification requires a clear and reasonably close view (to accurately judge size or to see the enlarged scutes on the knee), and many animals were only seen fleetingly or at a distance. Because we doubted that the forestry workers and local hunters with whom we spoke reliably distinguished this armadillo from the smaller but otherwise externally similar *D. novemcinctus,* we did not collect second-hand information about *Dasypus* species.

Dasypus novemcinctus Linnaeus

VOUCHER MATERIAL: AMNH 266483, 267012; MNHN 1995.953. Total = 3 specimens.

IDENTIFICATION: Our three vouchers conform in all qualitative external and cranial characters with the descriptions of this species by Husson (1978) and Wetzel and Mondolfi (1979). For comparison with Wetzel and Mondolfi's summary of quantitative data from *Dasypus novemcinctus* (op. cit.: table 1), the external measurements of our only adult specimen (AMNH 267012, female) were 506 × 380 × 95 × 51 mm, and it weighed 4.8 kg. The shell of AMNH 267012 was not preserved, but the other two specimens (both subadults with unfused basicranial sutures and incompletely erupted dentitions) each have nine movable bands, of which the fourth has 57 (MNHN 1995.953) or 60 (AMNH 266483) scutes. The condylonasal length of the skull of AMNH 267012 is 102.4 mm, the zygomatic width 44.8 mm, and the mastoidal width 29.0 mm; this specimen has seven paired maxillary teeth and eight paired mandibular teeth.

FIELD OBSERVATIONS: We heard armadillos crashing through the undergrowth or caught brief glimpses of them as they fled almost every night; most were probably *Dasypus novemcinctus* (usually the commonest rain-

forest armadillo throughout its extensive geographic range; Emmons, 1990, 1997), but it was impossible to make certain identifications in such cases. Our three vouchers were all shot at night in primary forest, at both well-drained and swampy sites. Numerous unambiguous sightings (many of which were not recorded) indicate that this species is common in all local habitats including primary forest and secondary growth. All of our observations were of solitary individuals. Although most sightings were nocturnal, we occasionally encountered nine-banded armadillos in the late afternoon, usually an hour or less before dusk.

Priodontes maximus (Kerr)

We only saw the giant armadillo once, on the night of 27 October 1994, when A. L. Peffley and RSV encountered a large (ca. 1 m HBL) adult of unknown sex excavating a mound of dead wood beside a rotting log in primary forest near a small stream at ca. 20: 00 hours. Alarmed by our headlights, it fled uphill toward a large treefall, where we were unable to follow in the dense undergrowth. Bushnegro forestry workers have sometimes pointed out burrows and excavations said to be made by this species to P. Petronelli (personal commun., 1993); according to them, collared peccaries (*Pecari tajacu*) use the abandoned burrows of giant armadillos as nocturnal retreats. Only one individual is known to have been shot by local hunters, about ten years before our inventory fieldwork began.

Cyclopes didactylus (Linnaeus)

The only records of the pygmy anteater at Paracou are two sightings by P. Petronelli (personal commun., 1993), each of a single animal of unkown sex crossing a dirt road through our study area.

Myrmecophaga tridactyla Linnaeus

Four sightings of giant anteaters by local forestry workers were reported to us (P. Petronelli, personal commun., 1993). One animal was seen in savanna vegetation, the other three in the forest; all were seen in the daytime. Covering about ten years of human residence at Paracou, these scant observations suggest that this large and conspicuous diurnal species is very uncommon.

Tamandua tetradactyla (Linnaeus)

Although we encountered this species only in 1992, when what was perhaps a single individual was heard twice (tearing apart dead wood or termite nests in trees at night) and sighted once (walking down a road at 07:20 hours) during a two-day interval, tamanduas are apparently not uncommon locally. P. Petronelli (personal commun., 1993) estimated that they are typically seen about five or six times a year by local forestry workers.

Husson (1978) referred the tamanduas of the Guiana subregion to *Tamandua longicaudata* (Wagner), but we follow Wetzel's (1975) revision of *Tamandua* in regarding *longicaudata* as a junior synonym of *tetradactyla.* Wetzel's revision should be consulted for diagnostic characters, as well as for a discussion of the considerable geographic and nongeographic variation in coat color of this species. Although Wetzel's map (op. cit.: fig. 1) indicates that only partially vested, unvested, or melanistic specimens are known from French Guiana, our single sighting (by DPL in broad daylight at a distance of ca. 10 m) was of a yellow individual with a distinctly blackish vest.

Primates

Six species of primates are definitely known to occur at Paracou, or to have occurred there in the recent past, and a seventh species could be expected (see appendix 1). Unfortunately, the local primate fauna has been decimated by uncontrolled hunting, a process that accelerated following completion of the new asphalt highway from Kourou to Sinnamary in 1992. Even at the beginning of our fieldwork in 1991, however, spider monkeys (*Ateles paniscus*), sakis (*Pithecia pithecia*), and capuchins (*Cebus* sp.) were rare. By 1994 (our last field season), only howlers (*Alouatta seniculus*) and tamarins (*Saguinus midas*) were commonly heard or seen in the vicinity of our camp, although capuchins could still be found a few kilometers away. Squirrel monkeys (*Saimiri sci-*

ureus) have probably always been local vagrants, not regular residents.

Thus, we never had the opportunity to census an intact primate community at Paracou, and some of the observations cited below were necessarily recorded at second hand. Fortunately, all Guianan primates are easily identified by obvious external characters (Emmons, 1990, 1997), so the likelihood of mistakes in the second-hand identifications we cite is remote.

Saguinus midas (Linnaeus)

VOUCHER MATERIAL: AMNH 266481, 266482; MNHN 1998.699. Total = 3 specimens.

IDENTIFICATION: Our three vouchers correspond exactly with Husson's (1978) detailed description of this species, which was based on topotypic material from Surinam. In particular, the diagnostic external markings of golden-handed tamarins—bright orange (sometimes reddish or yellow) hands and feet that contrast with the blackish limbs—are conspicuous in our vouchers as they are in all specimens referred to this taxon throughout the Guiana subregion of Amazonia (Hershkovitz, 1977). For comparison with published measurement data (Husson, 1957, 1978; Napier, 1976; Hershkovitz, 1977), selected external and craniodental dimensions (mm) of our two adult female vouchers are: head-and-body length 258, 285; length of tail 425, 440; length of hindfoot 77, 80; ear 36, 37; condylobasal length 38.9, 41.2; orbital breadth 28.7, 29.1; postorbital constriction 24.3, 25.6; zygomatic breadth 33.3, 34.8; maxillary toothrow (crown length C–M2) 12.8, 12.9.

The black-handed tamarins that occur south of the Amazon and east of the Xingu (including Ilha de Marajó) were long considered to be a distinct species from the golden-handed tamarins of the Guiana subregion (e.g., by Elliot, 1912; Cruz Lima, 1945; Hill, 1957; Cabrera, 1961). Hershkovitz (1977), however, treated golden- and black-handed tamarins as no more than subspecifically distinct; according to this authority, the correct name for the golden-handed Guianan tamarins is *Saguinus midas midas* (Linnaeus), whereas the black-handed tamarins of southeastern Amazonia should be called *S. midas niger* (E. Geoffroy). Apparently, the only published justification for treating these unequivocally diagnosable taxa as conspecific is the following (Hershkovitz, 1977: 207):

> The color of the cheiridia dictates the proffered hypothesis of racial differentiation. The pheomelanic or eumelanic cheiridia can be derived directly from the primitive agouti colored cheiridia . . . and either of the saturate patterns can switch to the other. Furthermore, presence of callitrichids on the Ilha de Marajó . . . discounts the probability of one race arising from the stock of another. It remains to be determined if tamarins with agouti cheiridia still persist on any of the innumerable islands of the lower Amazon.

Apparently, Hershkovitz judged the chromatic differences between *midas* (sensu stricto) and *niger* to be evolutionarily labile and predicted the existence of an extinct (or undiscovered) form that was (or is) intermediate in coloration and geography. However, the constancy of tamarin markings on opposite sides of the Amazon suggests that the character transformation in question is not evolutionarily labile, nor have populations with intermediate phenotypes yet been reported from any Amazonian islands.

According to Hershkovitz, only the coloration of the hands and feet distinguishes *midas* from *niger,* but his monograph contains no explicit comparison of these taxa in nonpelage characters. By contrast, subsequent research has shown that *midas* and *niger* have divergent dental measurements (Natori and Hanihara, 1992) and β_2-microglobulin DNA sequences (Canavez et al., 1999). Indeed, parsimony analysis of the β_2-microglobulin data provides compelling evidence that *midas* is more closely related to another species that occurs north of the Amazon, *S. bicolor* (Spix), than it is to *niger* on the opposite bank (Canavez et al., 1999).

In view of (1) the diagnosability of golden- and black-handed tamarins by bold and consistent pelage markings, (2) the existence of correlated divergence in nonpelage characters, and (3) clear indications from phylogenetic analysis that these taxa are not sister taxa, the currently accepted use of *midas* and *niger* as subspecies (Hershkovitz, 1977) or synonyms (Groves, 1993) is not defensible. Instead, we recognize the golden-handed tamarins of the Guiana subregion, *Saguinus*

midas, as a species distinct from the black-handed tamarins of southeastern Amazonia historically known by authors as *S. niger, S. tamarin,* or *S. ursulus* (see below).

REMARKS: Whereas most early authors used the epithets *tamarin* Link or *ursulus* Hoffmannsegg for the black-handed tamarin of southeastern Amazonia, Hershkovitz (1977) argued that the oldest applicable name for the zoological taxon in question is *niger* E. Geoffroy. Confusingly, the holotype of *niger* was clearly stated to have come from Cayenne (Geoffroy, 1803), far from the known range of black-handed tamarins. Although Hershkovitz reassigned the type locality to Belém, he did not examine Geoffroy's specimen, the identity of which is obviously problematic. Unfortunately, the holotype of *niger* (No. XXIV in Geoffroy's catalog) is lost: it was not listed in Rode's (1938) catalog of MNHN primate types, and it is not part of the current Paris museum collection (M. Tranier, personal commun.). Whether the original specimen of Geoffroy's *niger* was a melanistic individual of the golden-handed species collected at Cayenne or was a mislabelled example of the black-handed species is now impossible to determine. Nevertheless, the black-handed species is now widely and consistently known by the epithet *niger* E. Geoffroy, a usage that should be preserved in the interest of taxonomic stability. For that purpose, we hereby designate as neotype of *Sagouin niger* E. Geoffroy, 1803, an adult male specimen represented by a well-preserved skin and skull in the American Museum of Natural History, AMNH 96500, collected by A. M. Olalla on 2 November 1931 at Cametá on the Rio Tocantins, Pará, Brazil, from which locality a large series of topotypes is also available.

OTHER SPECIMENS EXAMINED: **Guyana**—*Cuyuni-Mazaruni,* Kartabo (AMNH 65159, 142936).

FIELD OBSERVATIONS: This is the commonest primate species at Paracou. We saw groups of tamarins daily, in both swampy and well-drained primary forest and in roadside secondary growth. In primary forest, tamarins were invariably sighted in the canopy or subcanopy, but we often saw them descend to within a few meters of the ground in roadside secondary growth; occasionally, groups were seen crossing dirt roads on the ground when the gap between trees on either side was too wide to leap. Unlike other primate species at Paracou, tamarins did not noticeably decline in density from 1991 to 1994, probably because they are not locally hunted for meat.

Alouatta seniculus (Linnaeus)

We heard howlers night and day throughout the course of our fieldwork at Paracou. Despite the audible evidence of their continuous presence, however, we seldom caught more than fleeting glimpses of this locally persecuted species. The few groups surviving in our study area never closely approached our camp, and they seldom ventured within the radius of our daily activities except to visit fruiting fig trees and other transient resources.

Ateles paniscus (Linnaeus)

Spider monkeys, always vulnerable to local extirpation by hunters because of their loud vocalizations, large size, highly prized meat, and low reproductive rate, have been scarce at Paracou for the last decade or more. P. Petronelli (personal commun., 1993) guessed that he had seen solitary individuals, never groups, on only five or six occasions since the early 1980s. We recorded only a single encounter with this species, when DPL saw a solitary individual in the canopy of well-drained primary forest near a fruiting fig tree on 2 July 1991; no noncaptive spider monkeys were seen or heard by us in later years.

Cebus apella (Linnaeus)

One or two species of *Cebus* were common at Paracou in the early 1980s (P. Petronelli, personal commun., 1993), but capuchins are now rarely seen or heard in the area. The older forestry workers are familiar with both a large and a small species, presumably *C. apella* and *C. olivaceus* (see appendix 1), but only *C. apella* has been definitely identified by sight at Paracou (P.-M. Forget, personal commun., 1994). We heard *Cebus* on several occasions in 1994 when our inventory activities extended ca. 3 km to

the NNW of camp (the limit of our sampling radius), but we caught no more than a brief glimpse of the animals as they fled in the distance and were not able to determine the species.

Pithecia pithecia (Linnaeus)

Although saki monkeys may once have been common at Paracou, P. Petronelli (personal commun., 1993) recalled only one sighting of this species prior to our inventory: a pair that he observed on 31 January 1991. Subsequently, we recorded three observations of *Pithecia pithecia* in our fieldnotes: (1) DPL saw a solitary individual on 3 July 1991; (2) RSV saw what might have been the same animal in the subcanopy of well-drained primary forest at 07:15 hours on 4 July 1991; and (3) Roland W. Kays saw two individuals leaping from tree to tree as he was walking along a dirt road at 16:30 hours on 6 August 1993. Silent and retiring by disposition, sakis may still linger in remote and seldom-visited parts of our study area, but their numbers have certainly been much reduced by hunting.

Saimiri sciureus (Linnaeus)

Squirrel monkeys have apparently been sighted only once at Paracou, when P. Petronelli (personal commun., 1993) encountered a group of 10–12 individuals on the edge of a small patch of savanna vegetation in the early 1980s. This species is probably a local vagrant that seldom strays far from the tangled growth at the forested margins of nearby savannas and rivers.

Carnivora

Ten species of carnivores are definitely known to occur at Paracou, and it is doubtful that any others occur in our study area except as rare vagrants (see appendix 1). Because all rainforest carnivores can be confidently identified by external characters (Emmons, 1990, 1997), and because many are uncommon and/or elusive, most of the information reported below was obtained by interviewing local forestry personnel.

Speothos venaticus (Lund)

We did not encounter bush dogs during our 1991–1994 fieldwork at Paracou, but P. Petronelli (personal commun., 1993) told us he had seen them twice in previous years: once as a group of four individuals, and another time as a group of three. A visiting photographer also saw a pack of seven bush dogs chase a paca across a road through the forest near our camp. All of these sightings were diurnal.

Herpailurus yaguarondi (Lacépède)

We did not see jaguarundis at Paracou, but P. Petronelli (personal commun., 1993) reported three sightings, all of solitary individuals on the ground in the daytime: one was crossing a road, one was near a stream in primary forest, and another was in secondary growth near the edge of a small patch of savanna vegetation.

Leopardus pardalis (Linnaeus)

Although ocelots are probably not uncommon at Paracou, they are rarely seen. We saw none, but local hunters have killed at least three in the last decade, one of which had the distinctively banded quills of *Coendou prehensilis* embedded in its neck and shoulders (P. Petronelli, personal commun., 1993).

Leopardus wiedii (Schinz)

Small spotted cats are often seen at night by local forestry workers (P. Petronelli, personal commun., 1993), and we recorded several fleeting encounters in our fieldnotes, but the identification of such observations is problematic. We have only two definite records of margays from our study area. (1) In 1993 we examined and measured an adult female, shot by a local hunter, that measured 563 × 427 × 124 × 54 mm and weighed 3.4 kg; the fur of the nape of the neck was reversed on this specimen, which likewise corresponded in other external characters to the descriptions provided by Pocock (1941), Emmons (1990, 1997), and Oliveira (1998). (2) On 19 September 1994, L. H. Emmons observed an emaciated male at a distance of only 6 m from 19:20 to 19:35 hours; the animal was encountered near a stream in pri-

mary forest, and half of its face was bristling with the large white quills of *Coendou prehensilis.*

Panthera onca (Linnaeus)

In the course of ten years' residence at Paracou, P. Petronelli (personal commun., 1993) told us that he had seen jaguars four times: twice in the daytime and twice at night, all in primary forest. Although we saw the distant eyeshine of large cats on several occasions, our only definite record of this species is based on the pugs of a young adult that L. H. Emmons observed along a dirt road on 13 October 1994.

Puma concolor (Linnaeus)

We did not see this species at Paracou in the course of our fieldwork, but P. Petronelli (personal commun., 1993) told us he had encountered pumas locally on four occasions, twice at night and twice in the daytime. One of the diurnal sightings was of an animal asleep on a high tree limb; another individual was found asleep between the buttresses of a big tree.

Eira barbara (Linnaeus)

Although tayras are common at Paracou, where they are sighted on average about 10–12 times a year by forestry workers (P. Petronelli, personal commun., 1993), we saw only three in the course of our fieldwork: RSV encountered a solitary individual in well-drained primary forest at 14:45 hours on 9 July 1991, DPL saw one crossing a dirt road in the daytime on 6 November 1992, and Nancy A. Voss sighted another in primary forest on an unrecorded date in 1994.

Galictis vittata (Schreber)

The only definite record of grisons within the limits of our study area is a sighting by P. Petronelli (personal commun., 1993), who observed a pair travelling together on the ground in primary forest in 1990. A large adult male that we found dead on a road near Sinnamary (ca. 12 km NNW of Paracou) in 1992 measured 553 × 155 × 92 × 32 mm and weighed 3.8 kg.

Nasua nasua (Linnaeus)

VOUCHER MATERIAL: AMNH 267605; MNHN 1995.959. Total = 2 specimens.

IDENTIFICATION: Our two vouchers, both juveniles, conform closely in pelage characters with the description of Surinamese specimens identified by Husson (1978) as *Nasua nasua vittata* Tschudi (1845), the type locality of which is in Guyana. Unfortunately, the appropriate trinomial designation for coatis from the Guiana subregion of Amazonia, if indeed a subspecific classification is necessary, remains to be convincingly determined.

Tate (1939) identified the lowland coatis of the Guiana subregion as *Nasua phaeocephala* J. A. Allen (1904)—apparently overlooking the availability of Tschudi's older name—and proposed a new name, *dichromatica,* for the montane population on Auyantepui in Venezuela. Subsequently, Cabrera (1958) referred all named forms of South American coatis to *N. nasua,* of which 11 subspecies were recognized as valid; in his classification, *phaeocephala* and *dichromatica* were both treated as subjective synonyms of *N. n. vittata.* According to Hershkovitz (1959), however, the oldest valid name for a Guianan coati is *Viverra quasje* Gmelin (1788), a name said to be based primarily on a Surinamese specimen described and illustrated by Seba (1734). Although Seba's specimen (BMNH 67.4.12.447), the presumptive type of *quasje,* was reported to be extant by Thomas (1892), we have found no evidence that it has been examined by any subsequent author.

Decker's (1991) revision of *Nasua* did not explicitly recognize any valid subspecies of *N. nasua,* but Gompper and Decker (1998) listed ten, including *N. n. vittata* (with *phaeocephala* and *dichromatica* as synonyms). Confusingly, Gompper and Decker listed *quasje* as a synonym of *N. n. nasua,* thus implying that two valid taxa of coatis occur in the Guianas. Without having undertaken a specimen-based revision of coati taxonomy, we are unable to evaluate the possible significance of any geographic variation in *Nasua nasua* that might occur in the Guiana subregion of Amazonia. However, it is clear from the literature reviewed above that if the French Guianan and Surinamese populations

TABLE 15
Measurements (mm) and Weights (kg) of Adult *Potos flavus* from Paracou[a]

	Males[b]	Females[c]
Head-and-body length	440 (416–470) 5	426 (395–449) 5
Length of tail	435 (414–465) 5	427 (380–468) 5
Length of hindfoot	95 (91–103) 5	91 (85–95) 5
Length of ear	40 (35–42) 5	41 (38–45) 5
Condylobasal length	78.6 (76.5–79.5) 5	74.8 (72.1–77.5) 5
Zygomatic breadth	58.1 (56.2–59.1) 5	55.2 (52.1–58.3) 5
Interorbital breadth	18.9 (17.8–19.8) 5	18.4 (17.9–19.4) 5
Postorbital breadth	22.6 (21.7–24.1) 5	21.7 (20.6–23.0) 5
Breadth of braincase	38.2 (36.8–40.4) 5	38.1 (36.6–40.3) 5
Maxillary toothrow	23.7 (22.8–24.9) 5	23.1 (21.4–24.3) 5
Length M1	4.5 (4.1–5.0) 5	4.4 (4.3–4.8) 5
Breadth M1	5.6 (5.3–6.1) 5	5.6 (5.3–5.8) 5
Weight	2.4 (2.1–2.9) 5	2.0 (1.5–2.6) 5

[a] Specimens age-classified after Kortlucke (1973): adults have fully erupted permanent dentitions and fused cranial (including basicranial) sutures. Summary statistics include the mean, the observed range (in parentheses), and the sample size.
[b] AMNH 267053, 267607, 267608; MNHN 1995.957, 1995.958.
[c] AMNH 265959, 266597, 266599, 267051; MNHN 1995.956.

(as represented by our vouchers and Husson's material) are distinct from the nominate form, the correct name for them may be *quasje* Gmelin, not *vittata* Tschudi. Clearly, resolving the application of Gmelin's name and reexamining Seba's original specimen should be a priority in any future revisionary study.

FIELD OBSERVATIONS: Coatis are uncommon at Paracou. P. Petronelli (personal commun., 1993) told us that he had seen coatis only twice in ten years, once in an experimental plot of disturbed forest (a group of two animals), and the second time in primary forest near a stream (a group of seven or eight); both sightings were in daytime. We encountered coatis only three times in the course of our inventory fieldwork. (1) On 15 August 1993, R. W. Kays sighted a group estimated to consist of about 20 individuals in a large tree at night; the tree was in well-drained primary forest, and the animals (including our two vouchers) were perching among the branches, about 20 m above the ground. (2) L. H. Emmons sighted a group of unknown size in swampy primary forest at 09:25 hours on 13 October 1994. (3) A. L. Peffley encountered a solitary individual of unknown sex in swampy primary forest at 09:00 hours on 18 October 1994.

Potos flavus (Schreber)

VOUCHER MATERIAL: AMNH 265956, 265958, 265959, 266597–266599, 267048, 267050, 267051, 267053, 267607, 267608; MNHN 1995.954–1995.958. Total = 17 specimens.

IDENTIFICATION: Our voucher material corresponds exactly in qualitative characters with Husson's (1978) description of topotypic specimens from Surinam. External and craniodental dimensions of Paracou specimens (table 15) likewise overlap those of topotypes measured by Husson (op. cit.: table 43).

Although partial revisions of *Potos flavus* by Thomas (1902), Kortlucke (1973), and Hernández-Camacho (1977) each recognized several subspecies as valid, there has been no geographically comprehensive study of kinkajou taxonomy to date. The Paracou population is presumably referrable to *P. f. flavus,* but the necessity for a trinomial classification remains to be convincingly demonstrated.

FIELD OBSERVATIONS: Kinkajous are by far the commonest carnivore at Paracou. We heard them squealing and crashing about in the canopy virtually every night throughout the course of our 1991–1994 fieldwork. All of our vouchers were shot at night in trees,

at estimated heights ranging from 10 to 30 m above the ground; recorded habitats include well-drained and swampy primary forest and roadside secondary growth. Although many apparently solitary individuals were encountered, kinkajous were also encountered foraging or travelling in pairs and larger groups. Collected specimens accompanied by information about group size include (1) an apparently solitary subadult female, (2) an apparently solitary lactating adult female, (3) a nonlactating and nonpregnant adult female accompanied by at least one other individual, (4) a juvenile male from a group of three individuals, (5) an apparently solitary subadult male, (6) an apparently solitary adult male, and (7) an adult male accompanied by at least one other individual. None of the six adult females we collected (in August and November) were pregnant.

Perissodactyla

Only one perissodactyl species occurs at Paracou, and no others are known from any Amazonian locality. Tapir dung, spoor, and the animal itself are unmistakable.

Tapirus terrestris (Linnaeus)

Although feces and tracks of this species are said to be commonly encountered in the more remote and swampy parts of our study area, the animal itself is seldom seen. During ten years' residence at Paracou, P. Petronelli (personal commun., 1993) encountered only one tapir, near a headwater stream of Crique Paracou in the daytime. Local hunters, however, are known to have killed at least two during the same interval.

Artiodactyla

Four rainforest artiodactyl species are known to occur at Paracou, and no others are expected (see appendix 1). All are unmistakable by external characters (Emmons, 1990, 1997) if a sufficiently good view is obtained.

Mazama americana (Erxleben)

Red brockets are apparently common at Paracou, local hunters having killed dozens in the last decade. According to P. Petronelli (personal commun., 1993), *Mazama americana* is primarily active at night; occasional daytime sightings are probably of individuals disturbed near their resting places. Although *M. americana* is believed to be locally more abundant than *M. gouazoubira* (below), we nevertheless obtained only two unambiguous sightings of red brockets in the course of our 1991–1994 inventory: (1) RSV observed a solitary individual stealthily retreating through the undergrowth of swampy primary forest in the mid-afternoon of 25 June 1991; (2) DPL saw a solitary individual in well-drained primary forest at 10:10 hours on 23 July 1993. Many unidentified deer whose eyeshine was detected in the forest undergrowth at night, or whose alarmed reactions (snorts and foot-stamps) were heard in the darkness, could have belonged to this species, or to the next.

Mazama gouazoubira (G. Fischer)

Voucher Material: AMNH 265960, 265961; MNHN 1995.960. Total = 3 specimens.

Identification: Both of our adult examples, one male (MNHN 1995.960) and one female (AMNH 265961), agree closely with Husson's (1978) qualitative description of Surinamese specimens that he identified as *Mazama gouazoubira nemorivaga.* Measurements of our vouchers (table 16) likewise correspond closely with morphometric data from *M. g. nemorivaga* summarized by Husson (1978: table 61) and Bisbal (1991: table II). In qualitative cranial traits, our two adult skulls conform with Medellín et al.'s (1998) characterization of northern South American populations of *M. gouazoubira,* except that the mesopterygoid fossae of both specimens have broadly U-shaped (not V-shaped) anterior margins.

Our vouchers are practically topotypes of *Cervus nemorivagus* F. Cuvier, the description of which was based primarily on specimens from Cayenne (Allen, 1915b; contra Miranda-Ribeiro, 1919). Although this taxon is currently considered a subspecies of *Mazama gouazoubira* (e.g., by Czernay [1987] and Grubb [1993], presumably following Ávila-Pires [1959]), no revisionary study based on extensive specimen data has, in fact, shown that the small grayish brockets

TABLE 16
Measurements (mm) and Weights (kg) of Adult *Mazama gouazoubira* from Paracou

	MNHN 1995.960	AMNH 265961
Sex	male	female
HBL	868	950
LT	102	85
HF	276	273
Ear	92	94
Condylobasal length	168.6	173.1
Maxillary toothrow[a]	51.9	51.6
Breadth M2[a]	11.8	12.1
Length of nasals	53.2	52.8
Interorbital constriction	33.8	37.2
Zygomatic breadth	73.0	75.8
Breadth of braincase	52.7	54.4
Weight	15.4	17.6

[a] Crown dimensions.

of the Guianas and those of Paraguay (the type locality of *gouazoubira*) are really conspecific. The character differences that Tate (1939) observed between specimens that he referred to *M. nemorivaga* and *M. simplicicornis* Illiger (= *M. gouazoubira*) should be carefully evaluated in any future taxonomic analysis of these deer.

REMARKS: The specific epithet of the gray brocket was originally spelled "*gouazoupira*" as noted by Grubb (1993). However, *gouazoubira* is the spelling that has been followed almost universally for many years, and we agree with Gardner (1999) that this usage should be maintained in the interest of nomenclatural stability.

FIELD OBSERVATIONS: Our three vouchers were all shot at night in well-drained primary forest. The still-nursing fawn (its stomach containing milk only) and the lactating adult female were collected together, whereas the young adult male (with antlers in velvet) was apparently solitary. In addition, L. H. Emmons observed what was probably a single individual on four different nights from 21 September to 10 October 1993 in well-drained primary forest.

According to P. Petronelli (personal commun., 1993), gray brockets are less common at Paracou than are red brockets, but they are nevertheless often sighted by forestry personnel, about 10–12 times per year on average.

Pecari tajacu (Linnaeus)

Collared peccaries were once common at Paracou, but although we often saw tracks and wallows (usually in parts of the forest distant from our normal inventory activities), we rarely saw the animals themselves. According to P. Petronelli (personal commun., 1993), this species is typically encountered locally in groups of 6–7 animals, always in the daytime, about 6–8 times per year on average.

Tayassu pecari (Link)

Groups of about 20 white-lipped peccaries have been sighted at Paracou on at least three occasions, all in the daytime (P. Petronelli, personal commun., 1993). Bushnegro forestry workers say that such groups visit the area about every four years. Although we did not see the animals themselves in the course of our 1991–1994 inventory fieldwork, L. H. Emmons observed fresh tracks of this species in primary forest on 12 October 1994.

RODENTIA

Rodents constitute the most diverse group of nonvolant mammals at Paracou, where we documented the occurrence of 22 species in six families: Sciuridae (2 species), Muridae (11 species), Erethizontidae (2 species), Dasyproctidae (2 species), Cuniculidae (1 species), and Echimyidae (4 species). An additional 11 species are known from other localities in French Guiana or Surinam (appendix 1), and some of these could also be expected to occur in our study area. Two species are described as new below.

Predictably, most Paracou rodent identifications proved to involve significant taxonomic problems, the resolution of which occupies the bulk of the following accounts. We define specimens to be *adult* if the permanent dentition is fully erupted, *subadult* if the molar dentition is completely erupted but the permanent premolars are not, and *juvenile* if one or more molars are incompletely erupted. Our quantitative comparisons of rodent crania and dentitions are based on the following measurements (figs. 33, 34).

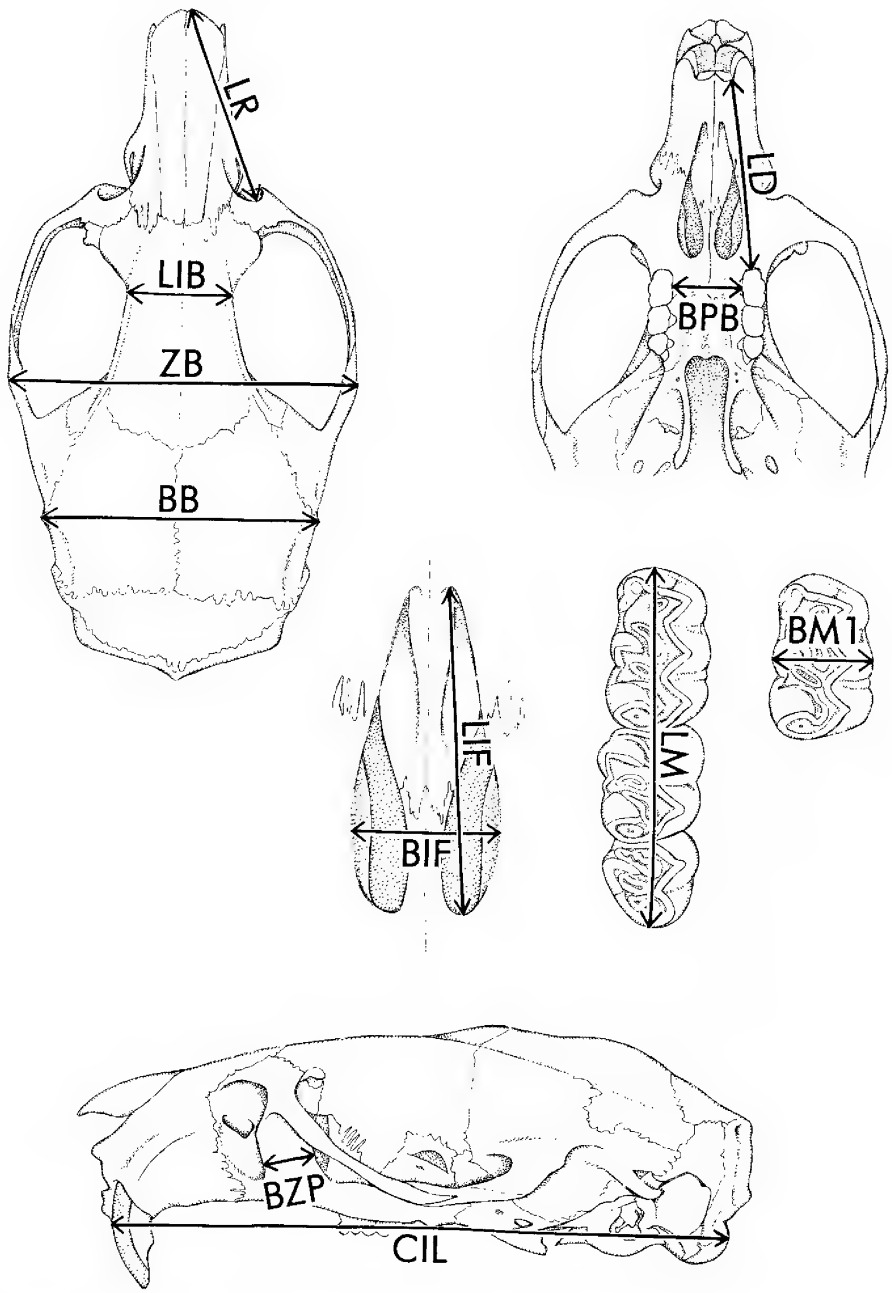

Fig. 33. Limits of 12 rodent craniodental measurements defined in the text.

Condylo-incisive Length (CIL): From the greater curvature of one upper incisor to the articular surface of the occipital condyle on the same side.

Length of Diastema (LD): From the crown of the first cheektooth to the lesser curvature of the incisor on the same side (except as noted in some tables, where the alveolar equivalent was measured).

Maxillary Toothrow (MTR): Crown length, from P4 to M3 (except as noted in some tables, where the alveolar equivalent was measured).

Length of Molars (LM): Crown length from M1 to M3.

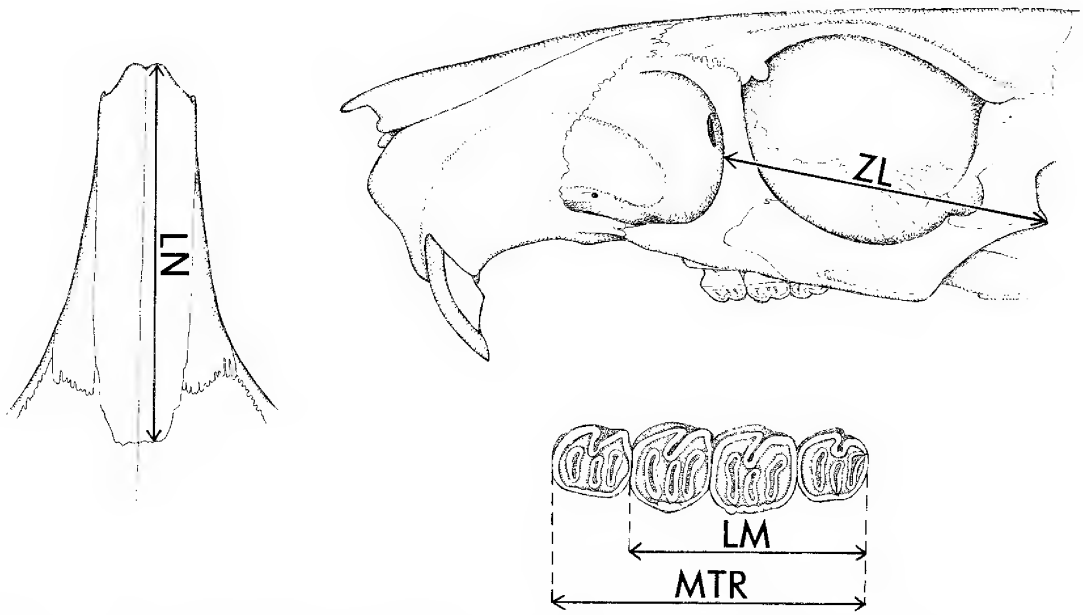

Fig. 34. Limits of four craniodental dimensions as measured for caviomorph rodents.

Breadth of M1 (BM1): Greatest crown breadth of the first maxillary molar.

Length of Incisive Foramen (LIF): Greatest anterior-posterior dimension of one incisive foramen.

Breadth of Incisive Foramina (BIF): Greatest transverse dimension across both incisive foramina.

Breadth of Palatal Bridge (BPB): Measured between the protocones of the right and left first maxillary molars (= "Anterior Palatal Breadth" of Voss and Angermann, 1997).

Breadth of Zygomatic Plate (BZP): Least distance between anterior and posterior edges of the zygomatic plate.

Length of Rostrum (LR): From the tip of one nasal bone to the posterior margin of the zygomatic notch on the same side.

Length of Nasals (LN): Greatest anterior-posterior dimension of one nasal bone.

Least Interorbital Breadth (LIB): Least distance across the frontal bones between the orbital fossae.

Breadth of Braincase (BB): Greatest transverse dimension across the braincase above and slightly behind the squamosal zygomatic processes.

Zygomatic Breadth (ZB): Greatest transverse dimension across the squamosal zygomatic processes (= "Posterior Zygomatic Breadth" of Voss and Angermann, 1997).

Zygomatic Length (ZL): From the posterior margin of the infraorbital foramen to the posterolateral corner of the zygomatic arch.

A few other measurements taken for special purposes are defined as necessary in the text and tables that follow. Because sexual dimorphism is an insignificant source of measurement variation in most rodents (e.g., see Straney [1978] and references cited by Voss [1988: 362]), we do not summarize morphometric data separately by gender.

Most of the larger rodents in the Paracou fauna (all sciurids, erethizontids, dasyproctids, and *Cuniculus paca*) can be identified at a distance by obvious external characters (Emmons, 1990, 1997), but most of the smaller rodents cannot be confidently identified without specimens in hand, and some closely related species cannot be unambiguously distinguished except from cleaned cranial material. In lieu of keys, we provide tabular summaries of diagnostic traits to facilitate identifications in some speciose genera.

Sciuridae

The two squirrels that we found at Paracou are the only species known to occur in French Guiana, Surinam, and Amapá; therefore, no future additions to the local sciurid

fauna are expected. Pending a revision of the complex nomenclature of these animals (M. de Vivo, in prep.), we follow the usages recommended by Husson (1978), who examined type material that we have not seen.

Sciurillus pusillus (E. Geoffroy)

VOUCHER MATERIAL: AMNH 269119. Total = 1 specimen.

IDENTIFICATION: Our voucher is almost topotypical of this species (originally described from specimens collected at Cayenne) and exhibits the reddish head, black ear tips, and white postauricular patches said to distinguish *S. p. pusillus* from other nominal taxa of South American pygmy squirrels (Anthony and Tate, 1935; Husson, 1978). The external dimensions of AMNH 269119, an adult female, were 109 × 74 × 28 × 14 mm; including two embryos *in utero,* this specimen weighed 51 g. Because fluid-preserved material of *Sciurillus* is rare in museum collections, we did not extract the skull of AMNH 269119 for measurement.

REMARKS: For the availability of names from Geoffroy's (1803) catalog (rejected by Wilson and Reeder, 1993: 831), see Hershkovitz (1955) and Holthuis (1963).

FIELD OBSERVATIONS: Our single voucher was shot by L. H. Emmons at 11:45 hours on 21 September 1994 as it fed on something growing on (or concealed beneath) the bark of a large *Inga* sp. (Mimosoideae) at a height of about 18 m in well-drained primary forest. In addition, we recorded fleeting diurnal observations of this species on five dates from 1991 to 1993; all of these sightings were of solitary individuals in trees in well-drained primary forest.

Sciurus aestuans Linnaeus

VOUCHER MATERIAL: AMNH 266485–266488, 266492, 266493, 267013, 267565; MNHN 1995.989–1995.991. Total = 11 specimens.

IDENTIFICATION: Our voucher material agrees closely in most details with Husson's (1978: 386–387) description of topotypic specimens from Surinam, but several points of comparison merit comment. (1) According to Husson, a few Surinamese examples have "very inconspicuous buffy yellow postauricular patches", but most do not; there is no trace of a postauricular patch on any specimen from Paracou. (2) Husson described the ventral coloration as "usually pale reddish brown, sharply separated from the colour of the dorsal surface, at least in about the middle of the body, but considerably less so in the anterior and posterior parts". By contrast, Paracou skins have clear (self-colored) orange fur on the chest, fading to buff or cream on the throat; some clear orange fur extends posteriorly along the ventral midline onto the abdomen, but most of the abdominal fur is gray-based, appearing grizzled like the flanks although much paler. (3) Some Surinamese specimens have substantially smaller measurements (op. cit.: table 62) than our vouchers (table 17), but it is possible that Husson included subadults in his sample.

TABLE 17
Measurements (mm) and Weights of Adult *Sciurus aestuans* from Paracou

	AMNH 266485	AMNH 266487	AMNH 266488	AMNH 267565	MNHN 1995.989
Sex	male	male	female	female	female
HBL	187	181	184	185	189
LT	180	—	188	190	172
HF	50	47	50	51	49
Ear	24	23	23	23	23
CIL	42.7	40.7	41.5	42.3	41.6
LD	13.0	12.0	12.6	12.7	12.7
MTR	7.5	7.6	7.2	7.6	7.4
BM1	2.2	2.3	2.1	2.2	2.1
LIF	3.1	3.3	3.0	2.9	3.2
BPB	5.7	—	5.8	6.1	5.5
LIB	15.9	15.0	16.3	16.2	16.1
ZB	27.5	26.5	27.0	28.9	27.8
Wt	200	180	179	210	175

This species (together with other members of the so-called *aestuans* group of *Sciurus*) was referred to the genus *Guerlinguetus* Gray by Allen (1915a), Tate (1939), Moojen (1942), Moore (1959), and others, but most recent authors have followed Cabrera (1961) in treating *Guerlinguetus* as a subgenus of *Sciurus.* Cabrera cited no published analysis of character data to support his opinion, however, and it seems probable that renewed morphological and molecular studies of Neotropical squirrels will advocate a return to the older generic usage.

Although the currently accepted synonymy (Hoffmann et al., 1993) for *Sciurus aestuans* implies that this species is distributed throughout eastern Amazonia to southeastern Brazil (including such forms as *alphonsei* Thomas, *garbei* Pinto, *henseli* Miranda-Ribeiro, *ingrami* Thomas, *poaiae* Moojen, and *roberti* Thomas; see Cabrera [1961] for bibliographic citations and type localities), we follow the last substantive specimen-based revisionary treatment of Amazonian squirrels (Moojen, 1942) in restricting *S. aestuans* to the Guiana subregion of Amazonia. In the Amazonian lowlands of southeastern Venezuela (geographically part of the Guiana subregion), however, *S. aestuans* is replaced by a different species that is usually identified (e.g., by Tate, 1939; Handley, 1976; Linares, 1998) as *S. gilvigularis* Wagner.

FIELD OBSERVATIONS: *Sciurus aestuans* is one of only three common diurnal rodents at Paracou. Most (9) of our 11 voucher specimens were shot in the daytime, and we recorded an additional 11 unvouchered daytime sightings in our fieldnotes; two trapped specimens were found at or near dawn, but might have been captured the preceding afternoon. With the exception of the latter, which were taken near ground level in Conibear and leghold traps set on tree trunks over a small stream, all of our observations of this species at Paracou were of animals perched in trees at heights of 3–30 m above the ground. Most individuals were solitary, but an adult male and an adult female were collected together on 13 August 1991. Habitat data accompanying specimens or sight records include 16 observations in primary forest at both well-drained and swampy sites, and 5 in more-or-less disturbed habitats.

MURIDAE

All of the genera of rainforest murids known to occur in the Guiana subregion of Amazonia are documented by vouchers collected at Paracou, including species of *Neacomys, Nectomys, Neusticomys, Oecomys, Oligoryzomys, Oryzomys,* and *Rhipidomys.* Although most Guianan murids can be provisionally identified to genus in the field by external characters described by Husson (1978) and Emmons (1990, 1997), we provide illustrations and supplementary information to facilitate field determinations of problematic taxa. Our anatomical terminology for muroid morphological characters follows that referenced or defined by Reig (1977), Voss (1988, 1993), Carleton and Musser (1989), Voss and Carleton (1993), and Musser et al. (1998).

Neacomys Thomas

The Neotropical spiny mice of the genus *Neacomys* have never been revised, and many aspects of their species-level taxonomy have long been problematic. The identification of spiny mice from the Guiana subregion of Amazonia is a case in point: although these have traditionally been identified as *N. guianae* (e.g., by Anthony, 1921a; Tate, 1939; Carvahlo, 1962; Husson, 1978; Genoways et al., 1981; Guillotin, 1982; Malcolm, 1990; Voss and Emmons, 1996), the diagnostic morphological characters and geographic range of this species are not documented in the literature. In his original description, Thomas (1905: 310) compared *N. guianae* only with *N. spinosus* (Thomas, 1882), stating that the new species was very similar but "conspicuously smaller". However, size does not distinguish *guianae* from such other diminutive forms as *tenuipes* Thomas (1900), *pusillus* Allen (1912), and *pictus* Goldman (1912). Musser and Carleton (1993) listed *N. guianae, N. pictus, N. spinosus,* and *N. tenuipes* (including *pusillus*) as valid species, but the recent description of two additional species from western Amazonia (*N. minutus* and *N. musseri*), together with sequence comparisons showing high levels of genetic differentiation among several undescribed mtDNA clades of spiny mice, suggests that the genus is much more diverse than previously recognized (Patton et al., 2000).

In order to identify our Paracou vouchers, we examined original descriptions of all nominal taxa of *Neacomys,* and we examined holotypes or paratypes of all the smaller named forms (*guianae, minutus, musseri, pictus, pusillus, tenuipes*). We tried to locate every Guianan *Neacomys* specimen currently housed in North American and European museums, and we measured representative

series to document morphometric variation within and among species. The results of our comparisons indicate that at least three distinct species are present in the Guiana subregion of Amazonia, of which two are new and occur sympatrically at Paracou. Because the very brief diagnoses of *Neacomys* provided by Thomas (1900), Gyldenstolpe (1932), and Ellerman (1941) are now insufficient as a basis for taxonomic inference, we rediagnose the genus here.

EMENDED DIAGNOSIS OF *NEACOMYS*: Small oryzomyines (sensu Voss and Carleton, 1993: 31) with coarsely grizzled yellowish-, reddish-, or grayish-brown dorsal fur containing short, grooved spines in addition to conventional guard hairs and underfur; ventral fur similar in composition to dorsal fur, but shorter and always contrastingly colored; pinnae small, dark, and sparsely haired; mammae eight in inguinal, abdominal, postaxial, and pectoral pairs; hindfoot with outer digits (I and V) much shorter than three middle digits (claw of dI not extending beyond middle of first phalange of dII, claw of dV not extending beyond first interphalangeal joint of dIV); claws of pedal digits II–V provided with ungual tufts of long whitish or silvery hairs that exceed the claws in length; tail sparsely haired (appearing naked except under magnification) with prominent epidermal scales in annular series, sometimes with a thin terminal pencil but never with a conspicuous tuft of long hairs at tip. Skull with prominently beaded supraorbital margins; interparietal large; palate long and wide, with prominent and often complex posterolateral pits flanking anterolateral margins of mesopterygoid fossa; parapterygoid fossae shallow (never deeply excavated above level of palate); alisphenoid strut absent (except as rare, usually unilateral variant); carotid circulation includes large stapedial artery (pattern 1 or 2 of Voss, 1988); tegmen tympani not overlapping posterior margin of squamosal (posterior suspensory process of squamosal absent); subsquamosal fenestra sometimes small but always present and usually patent. Upper incisors small, narrow, and opisthodont (never orthodont or proodont); lower incisor root contained in prominent capsular process on lateral surface of mandible; molars small and pentalophodont (mesolophs on M1 and M2 always well developed and fused to mesostyle on labial cingulum); M1/m1 without accessory roots.

Neacomys dubosti, new species

Figures 36, 37, 38B, 39A, 39C, 43

TYPE MATERIAL AND TYPE LOCALITY: The holotype, AMNH 267569, an adult female preserved as a fluid specimen with the skull extracted and cleaned, was collected at Paracou by R. W. Kays (original number: RWK 9) on 7 August 1993. No other material is known from the type locality, but all of the additional specimens we examined from French Guiana and Amapá are hereby designated as paratypes.

DISTRIBUTION AND SYMPATRY: Based on specimens we examined, *Neacomys dubosti* occurs in French Guiana, Amapá (Brazil), and southeastern Surinam (fig. 35). In Surinam, *N. dubosti* has been collected sympatrically with *N. guianae* (at the Sipaliwini Airstrip, Nickerie District), and it occurs sympatrically with another new species in French Guiana and Amapá (see the next account, below).

ETYMOLOGY: The specific epithet honors Gérard Dubost for his many contributions to knowledge of mammalian ecology and natural history in the lowland rainforests of French Guiana and Gabon. We are also grateful for his original suggestion of Paracou as the site for our mammal inventory, and for his subsequent support and advice throughout the course of our fieldwork there.

DIAGNOSIS: A small species of *Neacomys* (measurements in table 18) distinguished from other diminutive congeners by its short, usually unicolored tail; moderately short rostrum flanked by relatively shallow zygomatic notches; broad and strongly convergent interorbital region with highly developed, shelf-like supraorbital beads; broad and distinctly inflated braincase; short, convex-sided incisive foramina; carotid circulation pattern 1; M1 with undivided anterocone; mesoloph of M1 with more-or-less symmetrical connections to protocone and hypocone; persistently tubercular molar cusps; and a distinctive range of craniometric variation.

MORPHOLOGICAL DESCRIPTION: Dorsal pelage coarsely grizzled tawny- or reddish-

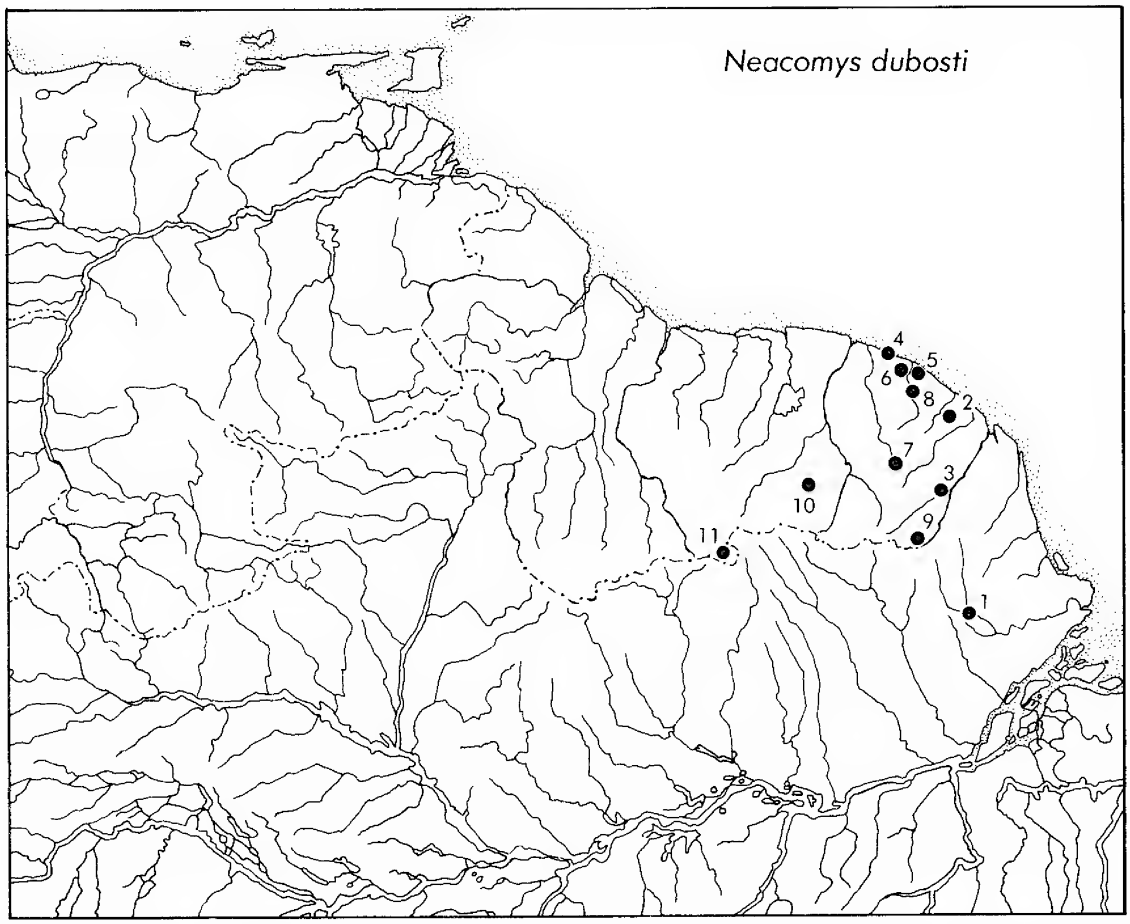

Fig. 35. Known collection localities of *Neacomys dubosti* based on specimens examined. **1,** BRAZIL, *Amapá,* Serra do Navio; **2,** FRENCH GUIANA, Cacao; **3,** FRENCH GUIANA, Camopi; **4,** FRENCH GUIANA, Iracoubo; **5,** FRENCH GUIANA, Paracou; **6,** FRENCH GUIANA, Piste St.-Élie; **7,** FRENCH GUIANA, Saül; **8,** FRENCH GUIANA, St.-Eugène; **9,** FRENCH GUIANA, Trois Sauts; **10,** SURINAM, *Marowijne,* Oelemarie; **11,** SURINAM, *Nickerie,* Sipaliwini Airstrip.

brown, somewhat paler along sides due to middorsal concentration of dark-tipped spines; ventral fur abruptly paler, sometimes pure white from chin to anus (e.g., CM 76840, MNHN 1983.412, USNM 46182), but more commonly suffused to a greater or lesser extent with buff or orange; ventral hairs usually pale to roots, very rarely with indistinctly gray bases (e.g., USNM 461571, 461590); broad lateral line of clear buff or orange separating dorsal and ventral pelage present in all specimens examined. Superciliary, genal, and some mystacial vibrissae extend behind pinnae when laid back against head. Dorsal surface of manus and pes covered by short pale fur in most specimens, but hairs over central metapodials sometimes indistinctly darker than those on digits and outer metapodials; claw of pedal digit I extending about one-half length of phalange 1 of adjacent digit II; claw of pedal digit V extending to but not beyond end of first phalange of adjacent digit IV; small but distinct hypothenar (lateral tarsal) plantar pad present on hindfoot of one fluid specimen (this trait is difficult to score reliably on dried skins). Tail about as long as combined length of head-and-body; almost always unicolored (dark above and below), but occasionally indistinctly paler ventrally at base (e.g., CM 76842, MNHN 1972.641); with small caudal scales (21 rows/cm near base of tail in one

TABLE 18
Measurements (mm) and Weights (g) of *Neacomys dubosti*

		French Guiana		
	Surinam[a]	Type[b]	Other specimens[c]	Amapá (Brazil)[d]
Sex	5 males, 2 females	female	10 males, 4 females	21 males, 4 females
HBL	78 (74–81) 7	80	71 ± 5 (64–81) 14	76 ± 4 (70–80) 25
LT	78 (71–83) 7	—	79 ± 7 (68–92) 14	79 ± 5 (70–85) 19
HF	21 (20–22) 7	21	20 ± 1 (19–21) 14	21 ± 1 (20–22) 25
Ear	15 (14–15) 7	14	12 ± 1 (11–14) 12	13 ± 1 (13–14) 25
CIL	18.2 (17.6–19.1) 7	18.4	18.4 ± 0.4 (17.8–19.2) 14	18.1 ± 0.6 (17.0–19.4) 24
LD	5.4 (5.1–5.8) 7	5.4	5.5 ± 0.3 (5.2–6.0) 14	5.3 ± 0.2 (5.0–5.9) 24
LM	2.7 (2.6–2.8) 7	2.8	2.7 ± 0.1 (2.6–2.8) 14	2.7 ± 0.1 (2.6–2.8) 25
BM1	0.8 (0.8–0.8) 7	0.9	0.8 ± 0.0 (0.8–0.9) 14	0.9 ± 0.0 (0.8–0.9) 25
LIF	3.0 (2.7–3.3) 7	2.8	3.0 ± 0.2 (2.7–3.3) 14	3.0 ± 0.2 (2.7–3.4) 25
BIF	1.5 (1.4–1.6) 7	1.4	1.6 ± 0.1 (1.4–1.7) 14	1.6 ± 0.1 (1.3–1.9) 24
BPB	2.2 (2.0–2.4) 7	2.3	2.2 ± 0.1 (2.0–2.3) 14	2.2 ± 0.1 (2.0–2.4) 25
BZP	1.8 (1.7–2.0) 7	2.1	2.0 ± 0.1 (1.8–2.1) 14	1.9 ± 0.1 (1.8–2.1) 25
LIB	4.5 (4.3–4.7) 7	4.6	4.6 ± 0.2 (4.3–4.9) 14	4.7 ± 0.2 (4.4–5.0) 25
LR	6.4 (6.1–6.9) 7	6.4	6.5 ± 0.2 (6.2–7.0) 14	6.4 ± 0.2 (5.9–6.7) 23
BB	10.3 (10.0–10.6) 7	10.7	10.4 ± 0.2 (10.1–10.8) 14	10.4 ± 0.2 (10.0–10.8) 25
Wt	14 (12–18) 6	16	16 (15–17) 3	14 ± 2 (11–19) 25

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: CM 76835–76837, 76839, 76840, 76842, 76843.

[b] AMNH 267569, a young adult female from Paracou.

[c] The mean ± one standard deviation, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: MNHN 1982.629, 1982.630, 1983.412, 1983.422, 1983.423, 1983.425, 1983.426, 1986.534, 1986.535, 1986.537, 1986.538, 1986.543, 1995.3226, 1998.1839.

[d] The mean ± one standard deviation, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: USNM 461563–461569, 461571, 461572, 461574–461576, 461579–461582, 461588, 461590, 461591, 461593–461595, 461601, 461604, 461612.

fluid specimen) forming relatively narrow annulations.

Skull with moderately short, tapering rostrum flanked by relatively shallow zygomatic notches; interorbital region broad, with strongly convergent lateral margins; supraorbital beads highly developed, projecting as small shelves over posterior orbits and continuing onto braincase as low temporal crests; braincase inflated, conspicuously domed, and very broad behind squamosal zygomatic processes. Incisive foramina relatively short (averaging about 57% of diastemal length), usually with distinctly convex lateral margins; zygomatic plate relatively narrow; carotid circulation with well-developed supraorbital ramus of stapedial artery (occupying squamosal-alisphenoid groove and sphenofrontal foramen; pattern 1 of Voss, 1988); subsquamosal fenestra smaller than postglenoid foramen but always distinct and patent; auditory bullae usually flask-shaped, tapering gradually from tympanic ring to unconstricted bony eustacian tubes.

First maxillary molar with undivided anterocone; anteroloph of M1 seldom distinct, usually fused labially with anterocone (anteroflexus usually distinguishable only as persistent internal fossette); mesoloph of M1 straight and slender, projecting labially from symmetrically Y-shaped junction with median mure, without disproportionate connection to hypocone; principal labial cusps (paracone, metacone) slightly reduced in size relative to lingual cusps (protocone, hypocone); principal cusps persisting as distinctly tubercular elements with moderate wear.

KARYOTYPES: Two specimens from Amapá (MNHN 1972.640, 1972.641) karyotyped by M. Tranier had diploid counts of 2N=62 chromosomes (as recorded on skin labels).

VARIATION: The three geographic samples

at hand, from Surinam, French Guiana, and Amapá (table 18), are very similar in most qualitative and quantitative characters. Instead, most of the variation in the material we examined (e.g., as noted parenthetically in the preceeding description) occurs as individual differences within local populations. However, resemblances are strongest between French Guianan specimens and a large series from the Serra do Navio in Amapá, Brazil. By contrast, our few Surinamese examples have slightly narrower molars and interorbital regions, and their supraorbital beads appear somewhat less developed as projecting shelves.

COMPARISONS: *Neacomys dubosti* could potentially be confused with two previously described congeners from northern South America—*N. tenuipes* and *N. guianae*—in addition to *N. paracou,* another new species described below. Selected qualitative contrasts among these four taxa are summarized in table 19, descriptive univariate statistics for measurements of representative series are provided in table 20, and the results of multivariate morphometric analyses are represented in figure 40 and table 21. More detailed, character-by-character comparisons are deferred to the next account. Patton et al (2000) recently described additional species of small-bodied *Neacomys* from western Brazil, but those bear no close resemblance to either *N. dubosti* or *N. paracou* and so are not treated in these accounts.

REMARKS: At least some of the specimens previously reported in the literature as *Neacomys guianae* by Carvalho (1962), Genoways et al. (1981), and Guillotin (1982) are probably referable to *N. dubosti,* but those authors did not provide the museum catalog numbers of relevant voucher material and we are therefore unable to associate confident species identifications with their observations.

OTHER SPECIMENS EXAMINED: **Brazil**—*Amapá,* Serra do Navio (USNM 461563–461569, 461571, 461572, 461574–461576, 461579–461582, 461584, 461588, 461590–461595, 461601, 461604, 461612); no other locality data (MNHN 1972.640, 1972.641). **French Guiana**—Cacao (MNHN 1983.426, 1986.534, 1986.535, 1986.537, 1986.538, 1986.541–1986.545), Camopi (MNHN 1983.403), Iracoubo (MNHN 1983.409), Piste St.-Élie km 16 (MNHN 1986.876, 1986.877), Saül (MNHN 1983.405–1983.407, 1983.422, 1983.423, 1983.425), St.-Eugène (MNHN 1995.3226–1995.3229, 1998.1835, 1998.1839), Trois-Sauts (MNHN 1982.629, 1982.630, 1983.410, 1983.412, 1983.414–1983.416). **Surinam**—*Marowijne,* Oelemarie (CM 76835–76837, 76839–76843); *Nickerie,* Sipaliwini Airstrip (CM 76846).

FIELD OBSERVATIONS: Our single specimen of *Neacomys dubosti* from Paracou was taken in a pitfall trap in creekside primary forest.

Neacomys paracou, new species

Figures 36, 37, 39B, 39D, 42B, 43

TYPE MATERIAL AND TYPE LOCALITY: The holotype, MNHN 1995.1020, an adult male preserved as a complete skeleton, was collected at Paracou on 23 August 1993 by Roland W. Kays (original number: RWK 30). All of the additional specimens we examined from Paracou (see Specimens Examined, below) are hereby designated as paratypes.

DISTRIBUTION AND SYMPATRY: Specimens that we refer to *Neacomys paracou* are from French Guiana, Surinam, Guyana, eastern Venezuela (Bolívar state), and Guianan Brazil (north of the Amazon and east of the Rio Negro) (fig. 41). Based on these records it would be reasonable to expect that the species occurs throughout the Guiana subregion of Amazonia, but we have not seen any material from the Amazonas federal territory of Venezuela. *Neacomys paracou* has been collected sympatrically with *N. guianae* in Guyana (at Kartabo), and with *N. dubosti* in Surinam (Oelemarie), French Guiana (Cacao, Paracou, Saül, St.-Eugène), and Amapá (Serra do Navio).

ETYMOLOGY: The species is named for our study area, treated as a noun standing in apposition to the generic name.

DIAGNOSIS: A small species of *Neacomys* (measurements in table 22) distinguished from other like-sized congeners by its very short outer pedal digits; short, unicolored tail; short rostrum flanked by relatively deep zygomatic notches; broad and usually strongly convergent interorbital region with well-

TABLE 19
Diagnostic Qualitative Comparisons among Four Species of *Neacomys*

tenuipes[a]	*guianae*[b]	*dubosti*[c]	*paracou*[c]
Hindfoot with long outer digits (claw of dV extends to end of first phalange of dIV, claw of dI extends at least to middle of first phalange of dII).	*Hindfoot* with short outer digits (claw of dV extends ca. 3/4 length of first phalange of dIV, claw of dI extends less than 1/2 length of first phalange of dII).	*Hindfoot* with long outer digits (claw of dV extends almost to end of first phalange of dIV, claw of dI extends to middle of first phalange of dII).	*Hindfoot* with very short outer digits (claw of dV extends ca. 2/3 length of phalange 1 of dIV, claw of dI barely extends beyond base of phalange 1 of dII).
Tail longer than head-and-body (ca. 115%) and usually distinctly bicolored, at least near base; caudal scales small.	*Tail* about as long as head-and-body, distinctly bicolored in some specimens; caudal scales small.	*Tail* about as long as head-and-body and usually unicolored (rarely indistinctly bicolored at base); caudal scales small.	*Tail* about as long as head-and-body and usually unicolored (sometimes indistinctly bicolored at base); caudal scales large.
Cranial characters include long rostrum flanked by shallow zygomatic notches; narrow, hourglass-shaped, or weakly convergent interorbital region; narrow zygomatic plates; short incisive foramina; and flask-shaped auditory bullae.	*Cranial characters* include moderately long rostrum flanked by shallow zygomatic notches; narrow, hourglass-shaped, or weakly convergent interorbital region; narrow zygomatic plates; short incisive foramina; and flask-shaped auditory bullae.	*Cranial characters* include moderately short rostrum flanked by shallow zygomatic notches; broad, strongly convergent interorbital region; narrow zygomatic plates, short incisive foramina; and flask-shaped auditory bullae.	*Cranial characters* include short rostrum flanked by deeper zygomatic notches; broad and usually strongly convergent interorbital region; broad zygomatic plates; long incisive foramina; and globular auditory bullae.
M1 approximately rectangular, with broad, often divided anterocone; labial and lingual cusps subequal and persistently tubercular; mesoloph slender, with symmetrical attachments to protocone and hypocone.	*M1* usually with narrower, undivided anterocone; labial cusps slightly smaller than lingual cusps; but dentition otherwise essentially similar to that of *N. tenuipes*.	*M1* usually with narrower, undivided anterocone; labial cusps slightly smaller than lingual cusps; but dentition otherwise essentially similar to that of *N. tenuipes*.	*M1* usually with very narrow, undivided anterocone; labial cusps much smaller than lingual cusps; principal cusps not persistently tubercular; robust mesoloph connected disproportionately to hypocone.

[a] Originally described by Thomas (1900) from a small series of skins, all of which were probably collected on the western slopes of the eastern Andes near Bogotá, Colombia. Material that we refer to this species is from premontane and lower montane habitats (400–1750 m elevation) in Colombia and northern Venezuela. Specimens examined: **Colombia**—*Antioquia,* 11.km S and 30 km E Cisneros (USNM 499543–499545), Quebrada del Oro (FMNH 70126), Sonsón (FMNH 70130, 70134), 25 km S and 22 km W Zaragoza (USNM 499541, 499546, 499547, 499549–499552, 499554, 499556–499559, 499578, 499579); *Boyacá,* Muzo (FMNH 71778); *Caldas,* Samaná (FMNH 71748, 71762, 71766); *Cundinamarca,* Paime (AMNH 69182); *Huila,* Acevedo (FMNH 71776). **Venezuela**—*Aragua,* Rancho Grande (USNM 517585–517588); *Distrito Federal,* Los Venados (USNM 371192); *Falcón,* Cerro Socopo (USNM 442241, 442242, 442245, 442246); *Miranda,* near Caracas (USNM 406046, 442236, 442237, 442239); *Yaracuy,* Minas de Aroa (USNM 442240).

[b] Originally described from a single specimen collected on the Demerara River, Guyana (Thomas, 1905). Material that we refer to this species is from lowland and premontane habitats (from near sea level to 850 m elevation) in eastern Venezuela, Guyana, and Surinam. Specimens examined: **Guyana**—*Mazaruni–Potaro,* Kartabo (AMNH 48141); "Demerara River" (BMNH 5.11.1.12 [holotype]). **Surinam**—*Nickerie,* Sipaliwini Airstrip (CM 76847); *Saramacca,* Tafelberg (CM 76848–76851). **Venezuela**—*Bolívar,* 45 km NE Icabarú (USNM 442247).

[c] See text for information about type material, type locality, and specimens examined.

developed and often shelf-like supraorbital beads; narrow, uninflated braincase; long, parallel-sided incisive foramina; carotid circulation pattern 1; M1 with narrow, undivided anterocone; mesoloph of M1 stout, often curving from and disproportionately connected to hypocone; principal molar cusps quickly worn to enamel loops, not persistently tubercular; and a distinctive range of morphometric variation.

TABLE 20
Comparative Measurements (mm) and Weights (g) of Representative Series of Four Species of *Neacomys*

	tenuipes[a]	*guianae*[b]	*dubosti*[c]	*paracou*[d]
HBL	83 ± 6 (72–97) 33	75 (64–85) 8	77 ± 4 (70–81) 33	75 ± 4 (70–83) 35
LT	96 ± 8 (74–108) 29	75 (67–81) 8	78 ± 5 (70–85) 26	75 ± 4 (65–81) 28
HF	22 ± 1 (20–24) 34	20 (19–20) 8	21 ± 1 (20–22) 33	20 ± 1 (18–21) 39
Ear	15 ± 2 (12–18) 33	14 (12–16) 7	14 ± 1 (13–15) 33	13 ± 1 (12–15) 39
CIL	19.0 ± 0.6 (17.8–20.2) 39	17.6 (17.0–18.0) 6	18.2 ± 0.6 (17.0–19.4) 32	18.0 ± 0.6 (17.0–19.1) 39
LD	5.5 ± 0.3 (4.9–5.9) 40	5.1 (4.9–5.4) 8	5.3 ± 0.2 (5.0–5.9) 32	5.2 ± 0.3 (4.7–5.8) 39
LM	2.8 ± 0.1 (2.7–3.0) 40	2.5 (2.4–2.6) 8	2.7 ± 0.1 (2.6–2.8) 33	2.7 ± 0.1 (2.5–3.0) 39
BM1	0.9 ± 0.0 (0.8–1.0) 40	0.8 (0.7–0.8) 8	0.9 ± 0.0 (0.8–0.9) 33	0.8 ± 0.0 (0.7–0.9) 39
LIF	3.1 ± 0.2 (2.5–3.5) 39	2.9 (2.7–3.2) 8	3.0 ± 0.2 (2.7–3.4) 33	3.4 ± 0.2 (3.0–3.9) 39
BIF	1.6 ± 0.1 (1.3–1.8) 40	1.5 (1.4–1.7) 8	1.6 ± 0.1 (1.3–1.9) 32	1.5 ± 0.1 (1.3–1.7) 39
BPB	2.3 ± 0.1 (2.1–2.7) 39	2.3 (2.1–2.4) 8	2.2 ± 0.1 (2.0–2.4) 33	2.3 ± 0.1 (2.0–2.5) 38
BZP	1.9 ± 0.1 (1.6–2.2) 40	1.8 (1.6–1.8) 8	1.9 ± 0.1 (1.7–2.1) 33	2.2 ± 0.1 (1.9–2.6) 39
LIB	4.4 ± 0.2 (4.2–4.8) 40	4.2 (4.0–4.5) 8	4.7 ± 0.2 (4.3–5.0) 33	4.7 ± 0.2 (4.1–5.1) 39
LR	7.0 ± 0.3 (6.4–7.6) 39	6.4 (6.0–6.9) 8	6.4 ± 0.2 (5.9–6.9) 31	6.2 ± 0.3 (5.5–6.6) 38
BB	10.4 ± 0.2 (9.8–10.8) 38	9.8 (9.5–10.0) 6	10.4 ± 0.2 (10.0–10.8) 33	10.0 ± 0.2 (9.6–10.5) 39
Wt	17 ± 3 (12–22) 24	13 (10–16) 7	14 ± 2 (11–19) 32	14 ± 2 (10–19) 38

[a] The mean ± one standard deviation, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 69182; FMNH 70126, 70130, 70134, 71748, 71762, 71766, 71776, 71778; USNM 371192, 406046, 442236, 442237, 442239–442242, 442245, 442246, 499541, 499543–499547, 499549–499552, 499554, 499556–499559, 499578, 499579, 517585–517588.

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 48141; BMNH 5.11.1.12 [holotype]; CM 76847–76851; USNM 442247.

[c] The mean ± one standard deviation, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 267569 [holotype]; CM 76835–76837, 76839, 76840, 76842, 76843. USNM 461563–461569, 461571, 461572, 461574–461576, 461579–461582, 461588, 461590, 461591, 461593–461595, 461601, 461604, 461612.

[d] The mean ± one standard deviation, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 266542, 266544–266546, 266548–266550, 266552–266557, 267570, 267572, 267574–267577; MNHN 1995.1013–1995.1016, 1995.1018, 1995.1020; USNM 461570, 461577, 461578, 461583, 461585, 461586, 461596–461600, 461603, 461608, 461609.

MORPHOLOGICAL DESCRIPTION: Dorsal pelage coarsely grizzled tawny- or reddish-brown, somewhat paler along sides due to middorsal concentration of dark-tipped spines; ventral fur abruptly paler, often pure white from chin to anus, but sometimes with orange pectoral markings (e.g., AMNH 266548), or broadly suffused with orange (e.g., CM 76845); ventral hairs pale to roots in most specimens (rarely with indistinctly gray bases between the fore- and hindlegs; e.g., AMNH 266545); broad lateral line of clear buff or orange separating dorsal and ventral pelage in many specimens, but lateral line narrow or absent in others (e.g., AMNH 266542, CM 76844, MNHN 1986.285). Superciliary and genal vibrissae extending behind pinnae when laid back alongside head, but mystacial vibrissae consistently shorter, not extending much if at all behind pinnae on properly made-up skins. Dorsal surface of manus and pes covered with short pale fur, often with indistinctly darker markings over central metapodials; claw of pedal digit I extending less than one-half length of phalange 1 of adjacent digit II; claw of pedal digit V extending no more than three-fourths length of phalange 1 of adjacent digit IV; hypothenar (lateral metatarsal) plantar pad small but distinct in some specimens, indistinct or absent in others. Tail about as long as, or a little shorter than, combined length of head-and-body; unicolored (dark above and below), rarely indistinctly paler ventrally at base (e.g., AMNH 266548); with large caudal scales (15–18 rows/cm near the base of the tail in nine fluid specimens) forming coarse and conspicuous annulations.

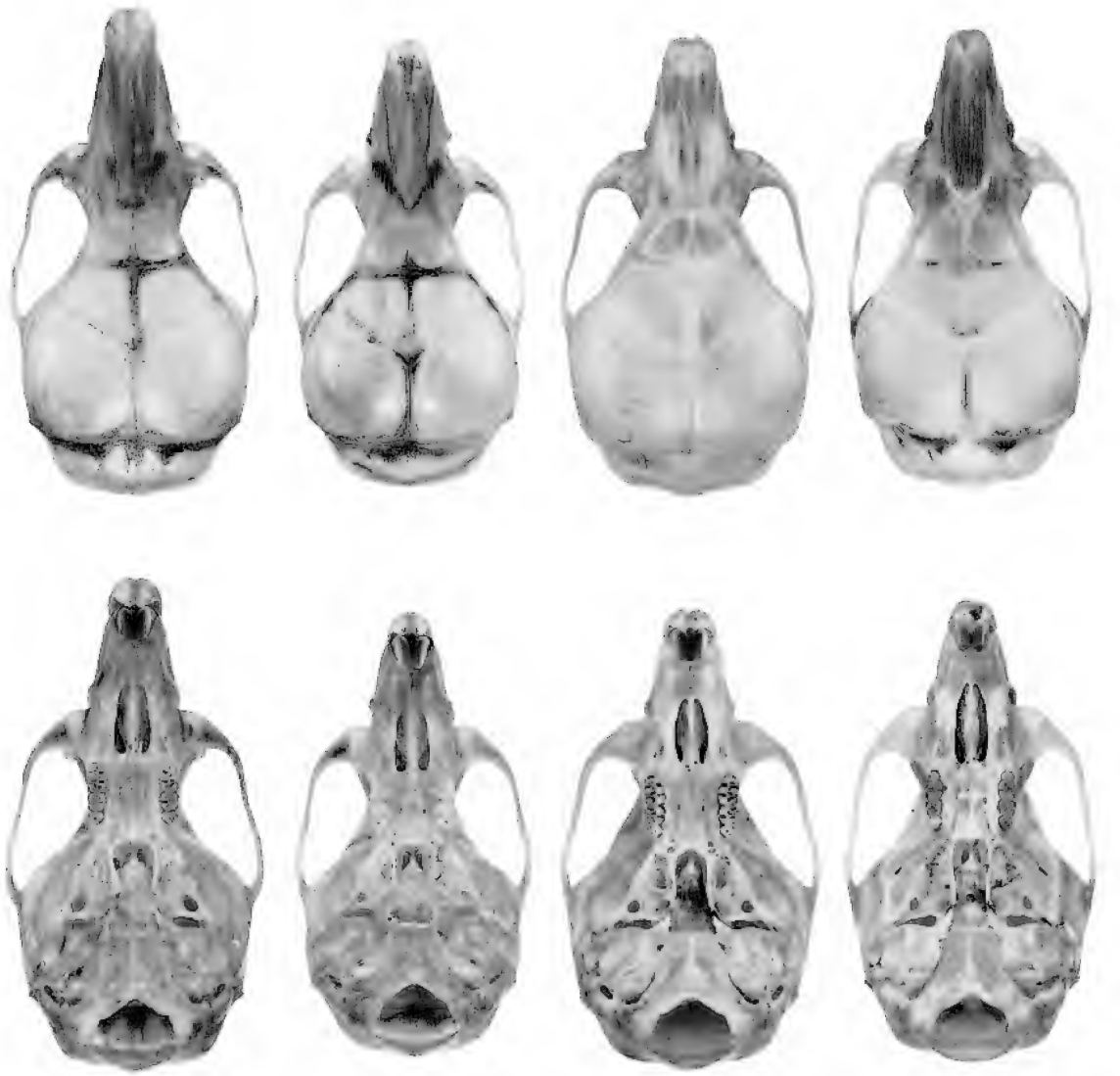

Fig. 36. Dorsal and ventral cranial views of four species of *Neacomys*. From left to right: *N. tenuipes* (FMNH 71778); *N. guianae* (CM 76850); *N. dubosti* (AMNH 267569, holotype); *N. paracou* (MNHN 1995.1020, holotype). All views about ×3.

Skull with very short rostrum flanked by moderately deep zygomatic notches; interorbital region broad and usually strongly convergent; supraorbital beads well developed, often projecting as small shelves over posterior orbits and continuing onto braincase as low temporal crests; braincase relatively narrow in most specimens and not conspicuously inflated. Incisive foramina relatively long (averaging about 65% of diastemal length) and narrow, usually with more-or-less parallel lateral margins; zygomatic plate relatively broad; carotid circulation with well-developed supraorbital ramus of stapedial artery (occupying squamosal-alisphenoid groove and sphenofrontal foramen; pattern 1 of Voss, 1988); subsquamosal fenestra often very small and sometimes occluded by internal flange of petrosal; auditory bullae usually globular, with spherical tympanic capsules and abruptly constricted bony eustacian tubes.

First maxillary molar typically with very narrow, undivided anterocone; anteroloph of

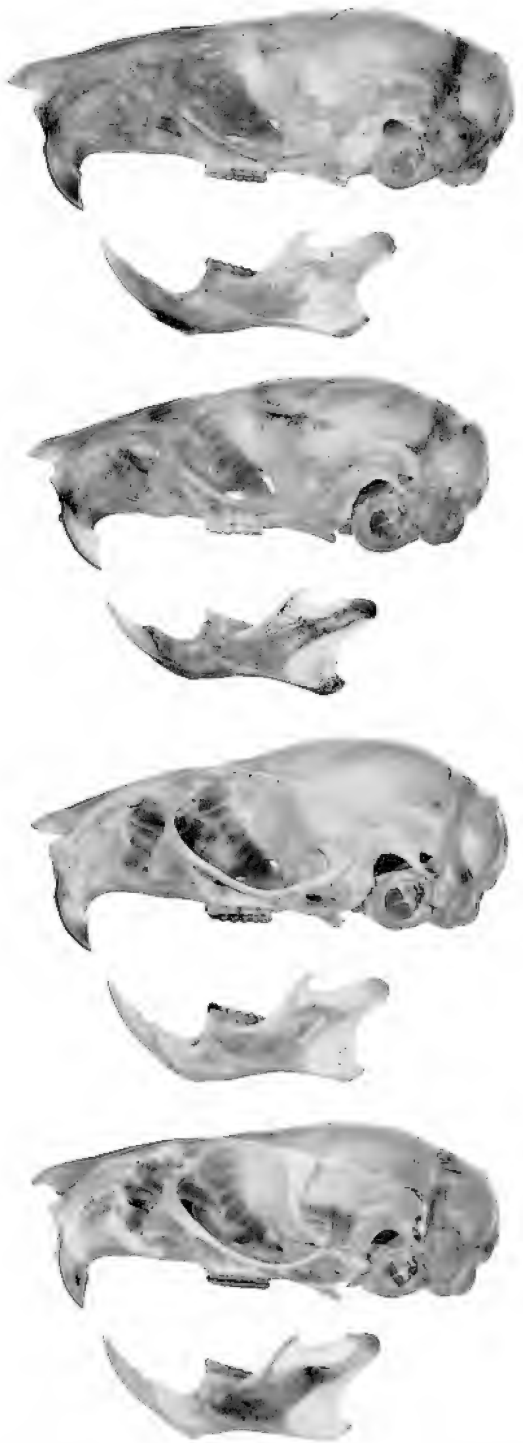

Fig. 37. Lateral cranial and mandibular views of four species of *Neacomys*. From top to bottom: *N. tenuipes* (FMNH 71778); *N. guianae* (CM 76850); *N. dubosti* (AMNH 267569, holotype); *N. paracou* (MNHN 1995.1020, holotype). All views about ×3.

TABLE 21

Results of Linear Discriminant Function Analysis of Craniodental Measurement Data from Four *Neacomys* Species Samples[a]

dubosti	0.0			
	(100)			
guianae	21.0	0.0		
	(0)	(100)		
paracou	31.3	31.9	0.0	
	(0)	(0)	(100)	
tenuipes	14.6	24.1	47.3	0.0
	(6)	(0)	(0)	(94)
	dubosti	*guianae*	*paracou*	*tenuipes*

[a] Upper matrix entries are generalized squared distances (Mahalanobis D^2) between species sample centroids computed from the pooled covariance matrix of log-transformed measurement data (the square roots of these values yield distances in units of within-sample standard deviations). Lower matrix entries (in parentheses) are percentages of specimens from row samples classified as column taxa using linear discriminant function scores. The analyzed specimens (N = 29 *dubosti*, 6 *guianae*, 37 *paracou*, and 36 *tenuipes*) are those with complete measurement data in the series identified by footnotes to table 20. These results suggest that the analyzed samples are morphometrically highly divergent from one another, with the exception of the incompletely distinguishable *dubosti/tenuipes* species pair.

M1 usually indistinct (fused with anterocone) even on unworn teeth; mesoloph of M1 very prominent (mesoloph/mesostyle complex sometimes rivalling paracone and/or metacone in size) and disproportionately connected to hypocone by median mure, arising anterolabially from that cusp in an uninterupted curve on most unworn teeth; principal labial cusps (paracone, metacone) distinctly smaller than lingual cusps (protocone, hypocone); all principal cusps quickly worn down to enamel loops, not persisting as distinctly tubercular elements in most adult dentitions.

KARYOTYPES: Two specimens of *Neacomys paracou* karyotyped by M. Tranier from "Cayenne, Rte. de Cacao", French Guiana (MNHN 1983.419, 1983.420) and another from Saül (MNHN 1983.418) had diploid counts of 2N=56 chromosomes (recorded on skin tags). The same diploid counts were obtained by E. Bach from chromosomal preparations of two Venezuelan specimens

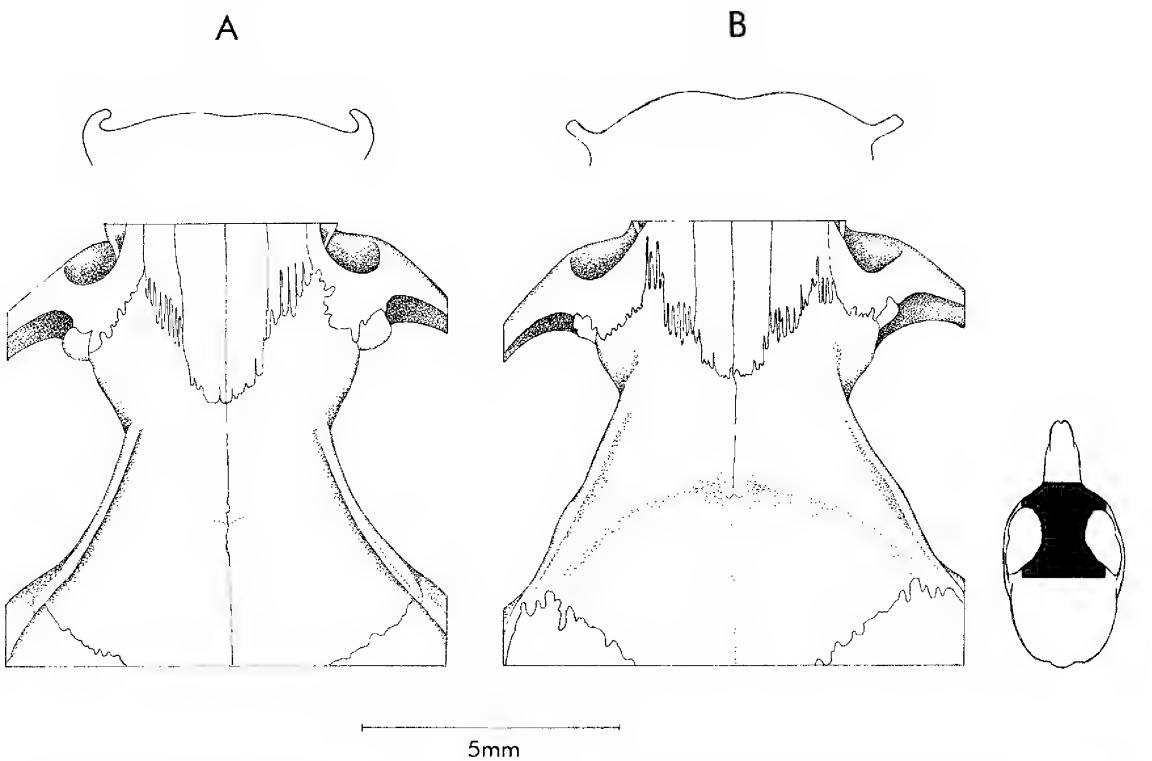

Fig. 38. Dorsal views and cross-sections of the interorbital region in *Neacomys tenuipes* (**A,** FMNH 71778) and *N. dubosti* (**B,** AMNH 267569, holotype). In most examined specimens of *N. tenuipes,* the interorbital region is relatively narrow and uninflated, with weakly convergent supraorbital margins; the supraorbital beads are usually strongly reflected and seldom form projecting shelves. By contrast, the interorbital region of *N. dubosti* is typically broader and more inflated, the supraorbital margins are more strongly convergent, and the supraorbital beads are more frequently developed as projecting shelves.

(AMNH 257270, MNHLS 8064) that were part of the series from San Ignacio Yuruaní originally misidentified by Voss (1991: table 23) as *N. tenuipes.*

VARIATION: Samples that we refer to *Neacomys paracou* are remarkably similar in morphological characters across a very large geographic range. The most metrically divergent series consists of three Venezuelan examples (from San Ignacio Yuruaní in eastern Bolívar state; table 22), which have longer hindfeet, slightly larger molars, and slightly longer rostrums than most Paracou specimens; broad overlap between these samples in most measured dimensions (together with the lack of other distinguishing characters), however, suggest that they are not specifically distinct. Specimens from two other geographically outlying samples (in the Brazilian states of Amazonas and Pará; measurements not tabulated) have less well-developed supraorbital beads than most topotypical specimens but do not appear to be morphometrically divergent or remarkable in other qualitative respects.

COMPARISONS: *Neacomys paracou* requires close comparisons with three other small species from northern South America, *N. dubosti, N. guianae,* and *N. tenuipes.* Of these, *dubosti, guianae,* and *paracou* occur in the Guiana subregion of Amazonia, where they have been collected sympatrically in all pairwise combinations (but never all three together). *Neacomys tenuipes* does not occur in the Guiana subregion, but its nomenclaturally crucial status as the oldest named species of small spiny mice compels us to include it in this comparative analysis.

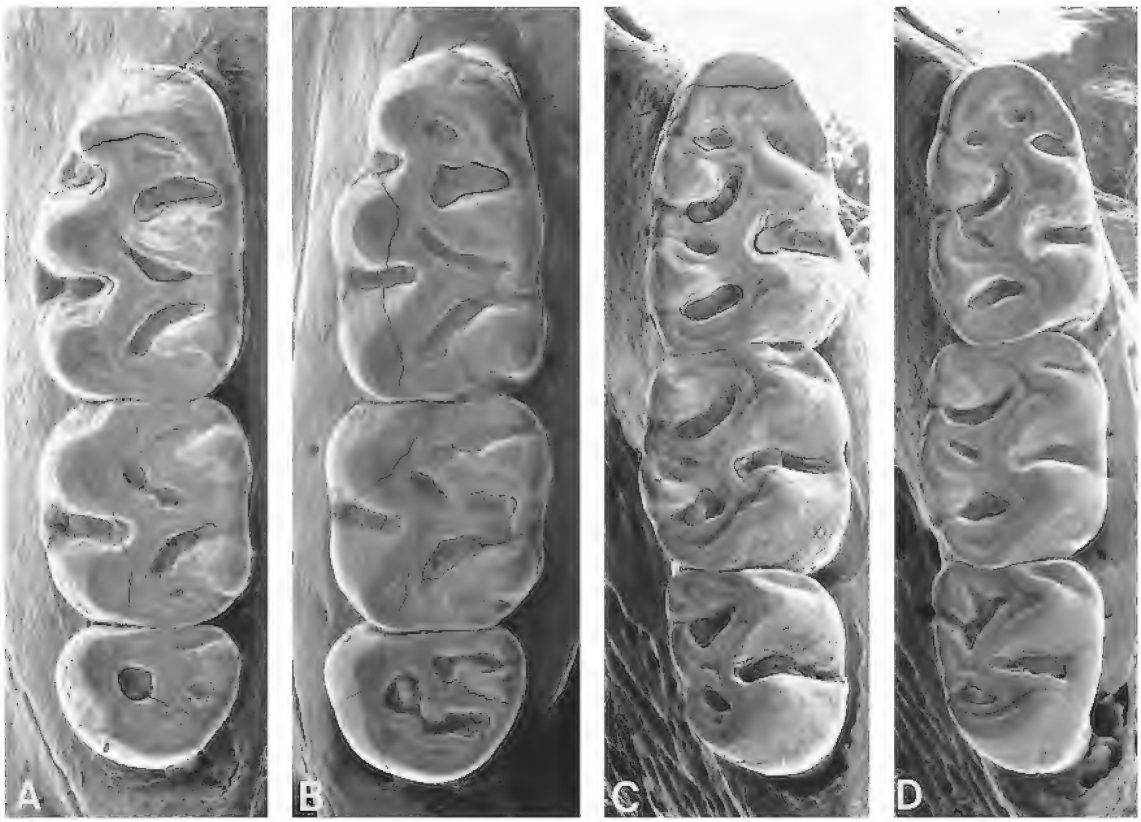

Fig. 39. Left maxillary toothrows (**A, B**) and right mandibular toothrows (**C, D**) of *Neacomys dubosti* (**A, C**; USNM 461580) and *N. paracou* (**B, D**; USNM 461609).

Although all small species of spiny mice are similar in most external characters, the morphology of the hindfoot and the tail can be used in combination to provide tentative field identifications. In *tenuipes* and *dubosti,* the outer pedal digits (dI and dV) are relatively long: the claw of dI extends almost or fully half the length of the first phalange of dII, and the claw of dV extends almost or fully to the end of the first phalange of dIV. By contrast, the claw of dI does not extend much beyond the base of the first phalange of dII in *guianae* and *paracou,* and the claw of dV in these two species does not extend more than about half the length of the first phalange of dIV. These proportional differences are easiest to see in fresh material, or in fluids, where the digits can be straightened and freely manipulated; in carelessly made-up skins (with twisted or bent toes), however, digital proportions can be hard to evaluate.

In specimens measured by the American method (total length and tail length [dorsal flexure to fleshy tip] measured in the field; head-and-body length calculated by subtraction), the tail is consistently longer than the head-and-body by a substantial amount (the ratio LT/HBL averaging about 115%) in *tenuipes,* but in the other three species the tail is about the same length as the head-and-body, on average. Unfortunately, the ratio of tail to head-and-body cannot be compared meaningfully among specimens measured by different protocols, and many specimens of *Neacomys* are captured with bobbed tails. Nevertheless, the contrast in tail length is visually obvious when comparing series of skins of *tenuipes* with those of *dubosti, guianae,* and *paracou.*

The tail is distinctly bicolored (dark above, pale below), at least near the base, in most specimens of *tenuipes,* but most specimens of *dubosti* and *paracou* have unicolored (all dark) tails. Unfortunately, the few available

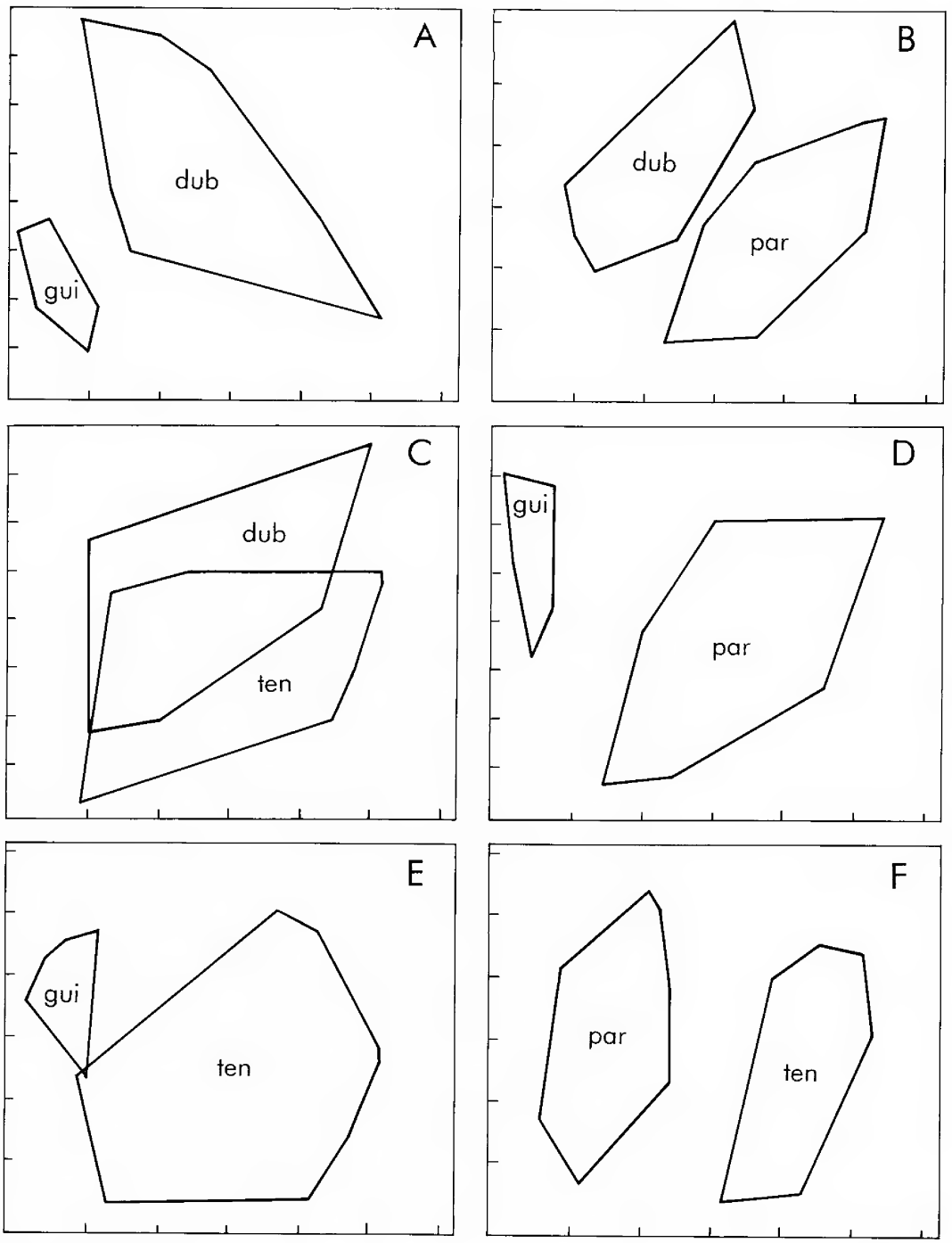

Fig. 40. Results of pairwise principal components analyses of representative samples of *Neacomys dubosti* (**dub,** N = 29), *N. guianae* (**gui,** N = 6), *N. paracou* (**par,** N = 37), and *N. tenuipes* (**ten,** N = 36). For each of the six analyses illustrated, principal components were extracted from the covariance matrix of log-transformed craniodental measurements of specimens with complete data in the series identified by footnotes to table 20. The first principal component is represented by the horizontal axis in each panel, the second principal component by the vertical axis; species samples are depicted as

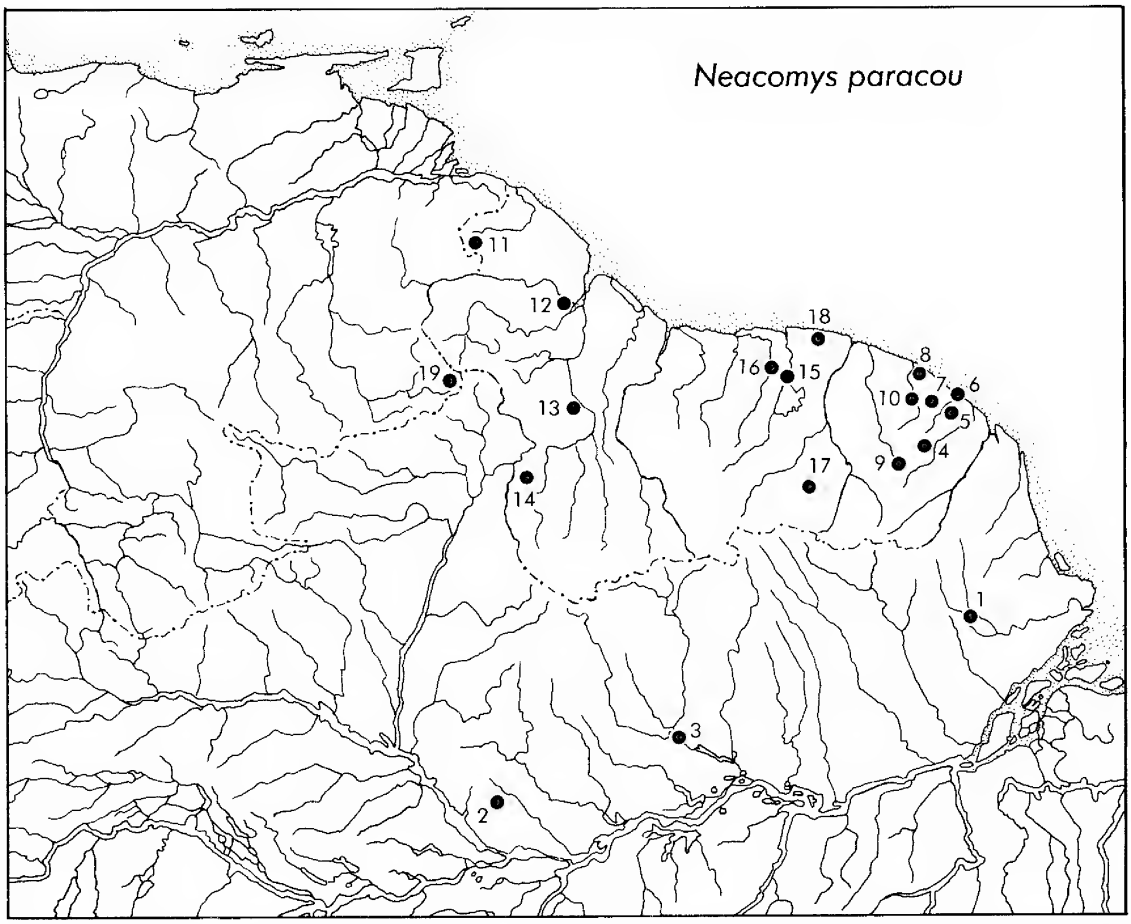

Fig. 41. Known collection localities of *Neacomys paracou* based on specimens examined. **1,** BRAZIL, *Amapá,* Serra do Navio; **2,** BRAZIL, *Amazonas,* 80 km N Manaus; **3,** BRAZIL, *Pará,* Cachoeira Porteira; **4,** FRENCH GUIANA, Arataye; **5,** FRENCH GUIANA, Cacao; **6,** FRENCH GUIANA, Cayenne; **7,** FRENCH GUIANA, Mont St.-Michel; **8,** FRENCH GUIANA, Paracou; **9,** FRENCH GUIANA, Saül; **10,** FRENCH GUIANA, St.-Eugène; **11,** GUYANA, *Barima-Waini,* Baramita; **12,** GUYANA, *Cuyuni-Mazaruni,* Kartabo; **13,** GUYANA, *Potaro-Siparuni,* Kurupukari; **14,** GUYANA, *Upper Takutu-Upper Essequibo,* Nappi Creek; **15,** SURINAM, *Brokopondo,* 18.5 km W Afobakka; **16,** SURINAM, *Brokopondo,* Locksie Hattie; **17,** SURINAM, *Marowijne,* Oelemarie; **18,** SURINAM, *Marowijne,* Perica; **19,** VENEZUELA, *Bolívar,* San Ignacio Yuruaní.

skins of *guianae* are too variable to characterize the species with confidence for this trait: whereas the type and two Surinamese specimens have tails that are distinctly bicolored at the base, four other specimens have indistinctly bicolored or unicolored tails.

In visual comparisons of dried skins, the

←

minimum convex polygons enclosing all referred specimens. Together, the first and second principal components accounted for 65% of the total variance in analyses A–D, 70% in analysis E, and 69% in analysis F. Species scores did not differ significantly on subsequent components (after the second) in analyses A, B, D, E and F, but the scores of *N. dubosti* and *N. tenuipes* differed significantly ($p \ll 0.01$ by 1-way ANOVA) on the fourth component (not shown) in analysis C.

TABLE 22
Measurements (mm) and Weights (g) of *Neacomys paracou*

	Venezuela[a]	Surinam[b]	French Guiana: Type and topotypes[c]	Amapá (Brazil)[d]
Sex	2 males, 1 female	4 males, 2 females	17 males, 8 females	12 males, 2 females
HBL	78 (72–87) 3	75 (69–82) 5	76 ± 3 (71–83) 21	73 ± 3 (70–80) 14
LT	82 (74–91) 2	72 (70–73) 3	75 ± 4 (67–81) 22	73 (65–80) 6
HF	21 (21–22) 3	19 (18–20) 5	19 ± 1 (18–21) 25	20 ± 1 (19–21) 14
Ear	14 (13–15) 3	14 (13–14) 4	13 ± 1 (12–15) 25	13 ± 1 (13–14) 14
CIL	18.9 (18.2–20.2) 3	17.9 (17.5–18.4) 5	18.1 ± 0.6 (17.0–19.0) 25	17.8 ± 0.6 (17.0–19.1) 14
LD	5.6 (5.2–6.1) 3	5.1 (5.0–5.3) 5	5.3 ± 0.3 (4.8–5.8) 25	5.1 ± 0.2 (4.7–5.5) 14
LM	2.8 (2.7–2.8) 3	2.6 (2.5–2.6) 5	2.6 ± 0.1 (2.5–2.8) 25	2.7 ± 0.1 (2.5–3.0) 14
BM1	0.8 (0.8–0.9) 3	0.8 (0.8–0.8) 5	0.8 ± 0.0 (0.7–0.9) 25	0.8 ± 0.0 (0.8–0.9) 14
LIF	3.4 (3.2–3.8) 3	3.2 (2.8–3.4) 5	3.4 ± 0.2 (3.0–3.9) 25	3.3 ± 0.2 (3.0–3.6) 14
BIF	1.4 (1.3–1.6) 3	1.5 (1.4–1.6) 5	1.5 ± 0.1 (1.3–1.7) 25	1.5 ± 0.1 (1.4–1.6) 14
BPB	2.2 (2.0–2.4) 3	2.2 (2.0–2.3) 4	2.3 ± 0.1 (2.0–2.5) 25	2.2 ± 0.1 (2.0–2.4) 13
BZP	2.1 (2.0–2.2) 3	2.1 (2.0–2.1) 5	2.1 ± 0.1 (2.0–2.4) 25	2.2 ± 0.2 (1.9–2.6) 14
LIB	4.8 (4.6–4.8) 3	4.6 (4.4–4.8) 5	4.7 ± 0.2 (4.1–5.1) 25	4.6 ± 0.2 (4.3–4.9) 14
LR	6.4 (6.1–6.8) 3	6.1 (6.0–6.4) 5	6.2 ± 0.2 (5.8–6.6) 24	6.2 ± 0.3 (5.5–6.6) 14
BB	10.4 (10.1–10.6) 3	9.9 (9.7–10.1) 5	10.0 ± 0.2 (9.7–10.5) 25	10.0 ± 0.2 (9.6–10.5) 14
Wt	16 (14–20) 3	14 (10–20) 5	14 ± 2 (11–19) 24	14 ± 2 (10–17) 14

[a] The mean, the observed range (in parentheses), and the sample size are tabulated for each measurement of the following series: AMNH 257269–257271.

[b] The mean, the observed range (in parentheses), and the sample size are tabulated for each measurement of the following series: CM 54016, 76838, 76844, 76845; FMNH 95642.

[c] The mean ± one standard deviation, the observed range (in parentheses), and the sample size are tabulated for each measurement of the following series: AMNH 266542, 266544–266546, 266548–266550, 266552–266557, 267569, 267570, 267572, 267574–267577; MNHN 1995.1013–1995.1016, 1995.1018, 1995.1020.

[d] The mean ± one standard deviation, the observed range (in parentheses) and the sample size are tabulated for each measurement of the following series: USNM 461570, 461577, 461578, 461583, 461585, 461586, 461596–461600, 461603, 461608, 461609.

caudal scales appear to be larger and to form coarser annulations in *paracou* than in the other three species, but this difference is hard to quantify because tails are stretched to varying degrees when skins are stuffed. Although we counted the number of scale rows per centimeter near the base of the tail on fluid specimens, only a few fluids were available for most species. Nevertheless, our data suggest that this character might be useful for field identifications: whereas nine adult fluid specimens of *paracou* from the type locality had 15–18 (mean = 16) scale rows/cm, the fluid holotype of *dubosti* had 21 rows/cm. We were not able to examine any fluid specimens of *tenuipes* or *guianae*.

We assessed species differences in cranial morphology by visual comparisons supplemented by measurements of representative samples (table 20). Although most statistical details of our morphometric analyses are necessarily omitted from this faunal report, the scatter plots in figure 40 depict patterns of multivariate divergence revealed by six pairwise principal components ordinations, and the matrix in table 21 summarizes the outcome of a linear discriminant function analysis with all species treated simultaneously. Both methods indicate that these taxa are craniometrically distinct in all pairwise combinations with the exception of *dubosti* and *tenuipes,* which have partially overlapping multivariate distributions. The following are the principal points of quantitative and qualitative cranial difference based on our visual and analytic comparisons.

When samples of skulls are lined up in comparative series, each species has a distinctive dorsal gestalt as a consequence of taxonomic variation in four anatomically adjacent and visually juxtaposed structures: (1) The rostrum varies in absolute and relative

length, being longest on average in *tenuipes* and shortest in *paracou*; the rostrum is of intermediate length in *guianae* and *dubosti*. (2) The zygomatic notches (dorsal emarginations of the maxillary bone flanking the base of the rostrum) vary in depth as a correlate of variation in the width of the zygomatic plate; the zygomatic notches are deepest and the zygomatic plates widest in *paracou,* whereas *tenuipes, guianae,* and *dubosti* have shallower zygomatic notches and correspondingly narrower zygomatic plates. (3) The interorbital region is relatively narrow, and the supraorbital beads are relatively weakly developed (seldom produced as shelf-like projections over the posterior orbits) in *tenuipes* and *guianae*; in these species, the modal interobital morphology could be described as weakly convergent (fig. 38A). By contrast, *dubosti* and *paracou* have relatively broader interorbits, and the supraorbital beads are more frequently developed as projecting shelves; their modal interorbital morphology is strongly convergent (fig. 38B). (4) The braincase is relatively broader and more inflated in *dubosti* than in any of the other three species.

Taxonomic variation in other quantitative and qualitative cranial traits also contributes to species recognition. The incisive foramina of *paracou* are longer in relation to the diastema (LIF averaging about 65% of LD) than those of *tenuipes, guianae,* and *dubosti* (in which this proportion averages about 56–57%), and subtle taxonomic differences in the shape of these diastemal perforations are also present. Thus, the foramina are relatively narrow in proportion to their length and usually have subparallel lateral margins in *paracou,* whereas the foramina are relatively broader with more convex or anteriorly convergent lateral margins in the other species.

Although the shape of the auditory bullae exhibits individual variation within most population samples, the bullae of *paracou* are more consistently globular in form, each consisting of a roughly spherical tympanic capsule that is usually abruptly constricted anteromedially to form narrow bony eustacian tubes (fig. 42B). By contrast, the bullae of *tenuipes, guianae* (fig. 42A), and *dubosti* are usually flask-shaped, each tapering gradually from the tympanic annulus to a relatively broader eustacian tube. Insufficient in itself for species diagnosis, this character is nevertheless useful for corroborating identifications when used in conjunction with other traits.

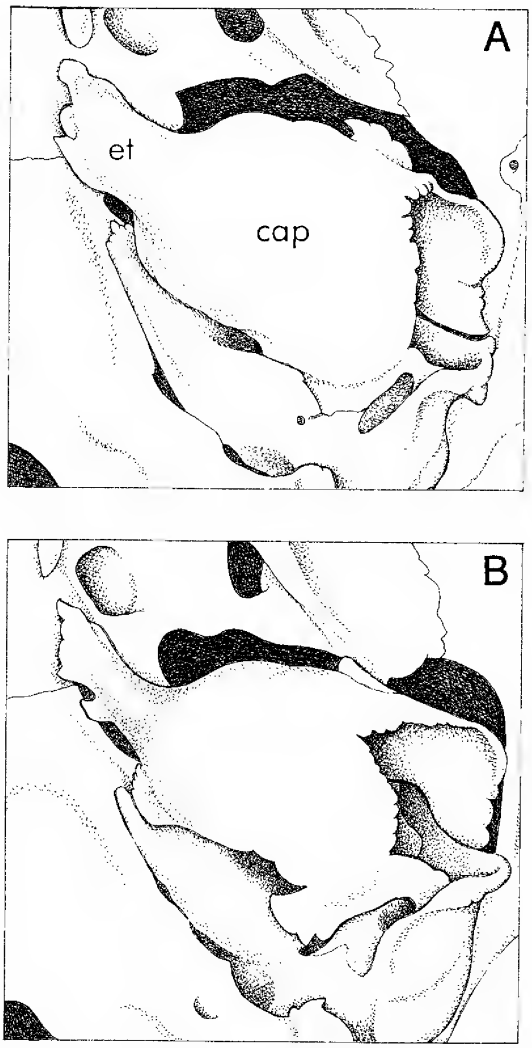

Fig. 42. Ventral views of the left auditory bulla in *Neacomys guianae* (**A,** CM 76850) and *N. paracou* (**B,** MNHN 1995.1020, holotype). In *N. guianae* the capsular part of the auditory bulla (**cap**) narrows gradually to merge with the bony eustacian tube (**et**), and the bulla is more-or-less flask-shaped. By contrast, the bulla is abruptly constricted anteromedially in *N. paracou,* resulting in a sharper transition between a more globular tympanic capsule and a narrower eustacian tube.

The morphology of the first maxillary mo-

Fig. 43. Occlusal morphology of the left first maxillary molar (M1) of *Neacomys* species. Left to right: *N. tenuipes* (USNM 499555), *N. guianae* (CM 76849), *N. dubosti* (USNM 461580), and *N. paracou* (USNM 461609).

lar also differs significantly among the four species (fig. 43). In *tenuipes,* M1 is more-or-less rectangular in outline because the anterocone is almost as broad as the paracone-protocone cusp-pair behind it. In many specimens with unworn dentitions (especially from the central Andean cordillera of Colombia; e.g., FMNH 70126, USNM 499555), the anterocone is deeply divided into anterolingual and anterolabial conules by an anteromedian flexus, and the anteroloph is large and distinct. The occlusal organization of the tooth is strikingly symmetrical, with subequal lingual and labial cusps that remain persistently tubercular with moderate wear. The mesoloph is a slender crest of enamel, perpendicular to the long axis of the tooth, that forms a Y-shaped junction with the median mure and lacks a disproportionate connection to either of the two principal lingual cusps (protocone and hypocone).

The modal morphology of M1 in *guianae* and *dubosti* is essentially similar to that seen in *tenuipes,* but differs in certain details. Thus, the anterocone is undivided and usually distinctly narrower than the protocone-paracone cusp-pair, giving the tooth a less rectangular and more egg-shaped outline, and the anteroloph is seldom distinct (the anteroflexus usually persisting, if at all, only as a small internal fossette). There is also a tendency, that is more marked in some specimens than in others, for the labial cusps (paracone and metacone) to be reduced in size relative to their lingual counterparts (protocone and hypocone), resulting in a less symmetrical occlusal design. In addition to these shape differences, the toothrow is absolutely shorter in *guianae* than in either *tenuipes* or *dubosti.*

The typical morphology of M1 in *paracou* differs in several respects from that seen in the other three species. The tooth is visibly narrower in relation to its length, on average, and the undivided anterocone is usually much narrower than the protocone-paracone cusp-pair behind it. In most specimens, this tooth exhibits a striking departure from bilateral symmetry, with the labial cusps being much reduced in size relative to their lingual counterparts, and with an enlarged mesoloph that runs obliquely and disproportionately from the hypocone to the labial cingulum. In addition, the principal cusps are not persistently tubercular because they are quickly worn down to enamel loops; thus, even moderately worn dentitions are essentially flat-crowned, lacking any significant occlusal relief.

REMARKS: Specimens that we examined and determined to be *Neacomys paracou* include at least some of the material previously

identified as *N. guianae* by Anthony (1921a), Husson (1978), Guillotin (1982), Malcolm (1990), and Voss and Emmons (1996: appendices 4 and 5). It is probable that other literature records of *N. guianae* are also based partly or entirely on specimens of *N. paracou,* which appears to be the commonest and most widespread of the three *Neacomys* species now known from the Guiana subregion of Amazonia.

Specimens Examined: **Brazil**—*Amapá,* Serra do Navio (USNM 461570, 461577, 461578, 461583, 461585, 461586, 461596, 461597–461600, 461603, 461605, 461608, 461609); *Amazonas,* 80 km N Manaus (USNM 580008–580011); *Pará,* Cachoeira Porteira (USNM 546277–546281). **French Guiana**—Arataye (MNHN 1986.284–1986.286, 1986.870–1986.875), Cacao (MNHN 1986.536, 1986.539), Cayenne (MNHN 1983.419, 1983.420), Mont St.-Michel (MNHN 1983.411), Paracou (AMNH 266542, 266544–266546, 266548–266550, 266552–266557, 267570, 267572, 267574–267577; MNHN 1995.1013–1995.1022 [type series]), Saül (MNHN 1983.405, 1983.418, 1983.421, 1983.424), St.-Eugène (MNHN 1998.1834, 1998.1836–1998.1838). **Guyana**—"River Supinaam" (BMNH 10.5.4.22); *Barima-Waini,* Baramita (ROM 100947); *Cuyuni-Mazaruni,* Kartabo (AMNH 42893, 64146, 64147, 142821, 245037); *Potaro-Siparuni,* Kurupukari in Iwokrama Reserve (BMNH 1997.44, 1997.46); *Upper Takutu-Upper Essequibo,* Nappi Creek in Kanuku Mountains (ROM 31760). **Surinam**—*Brokopondo,* 18.5 km W Afobakka (CM 54016), Locksie Hattie on Saramacca River (FMNH 95642, 95643); *Marowijne,* Oelemarie (CM 76838, 76844), Perica (CM 76845). **Venezuela**—*Bolívar,* San Ignacio Yuruaní (AMNH 257269–257271).

Field Observations: All of our inventory records of *Neacomys paracou* are based on collected specimens (N = 29), of which 17 (62%) were taken in Sherman traps, 8 (28%) were taken in pitfalls, 3 (10%) were taken in Victor rat traps, and 1 was shot. Most trapped specimens were found at dawn, but a single specimen was found in the late afternoon in a pitfall that had been checked earlier on the same day. Fourteen specimens (48% of the total) were shot or trapped in secondary vegetation, 10 (35%) were trapped in well-drained primary forest, and 5 (17%) were trapped in swampy primary forest. All specimens were collected at or near ground level. Of the 18 Sherman- or Victor-trapped specimens, most were taken in dense undergrowth near woody shelter: under logs (6 specimens), on top of logs (3), among stilt roots (3), beside logs (2), under piled branches (2), inside a hollow log (1), and at the base of a tree (1).

Nectomys melanius Thomas

Figures 44, 45B, 46B, 47B

Voucher Material: MNHN 1998.680, 1998.681. Total = 2 specimens.

Identification: The genus *Nectomys* was last revised by Hershkovitz (1944), who recognized all of the material he examined as belonging to one or the other of two polytypic species assigned to different subgenera, *Nectomys* (*Nectomys*) *squamipes* (Brants) and *N.* (*Sigmodontomys*) *alfari* (J. A. Allen). Current usage (summarized by Musser and Carleton, 1993), however, recognizes *Sigmodontomys* and *Nectomys* as full genera, the former with two valid species (*S. alfari* and *S. aphrastus*) and the latter with three (*N. palmipes, N. parvipes,* and *N. squamipes*). Only *Nectomys* (sensu stricto) is known to occur in Amazonia, *Sigmodontomys* being restricted to trans-Andean and Venezuelan coastal rainforests (Voss and Emmons, 1996: table 1).

Nectomys squamipes melanius was originally described by Thomas (1910: 185–186), who considered it "the Guianan representative of the Brazilian water rat, *N. squamipes,* but . . . distinguishable by its darker dorsal color and smaller skull and teeth." Thomas's account was based on a small series of specimens from Guyana and Surinam, but additional material identified as *melanius* was subsequently described by Hershkovitz (1944) and Husson (1978). Whereas both Hershkovitz and Husson followed Thomas in treating *melanius* as a valid subspecies of *N. squamipes* (Brants, 1827), Tate (1939) synonymized *melanius* with *N. s. palmipes,* a taxon that was originally described (as a full species) by Allen and Chapman (1893) from Trinidad. Petter (1979) subsequently de-

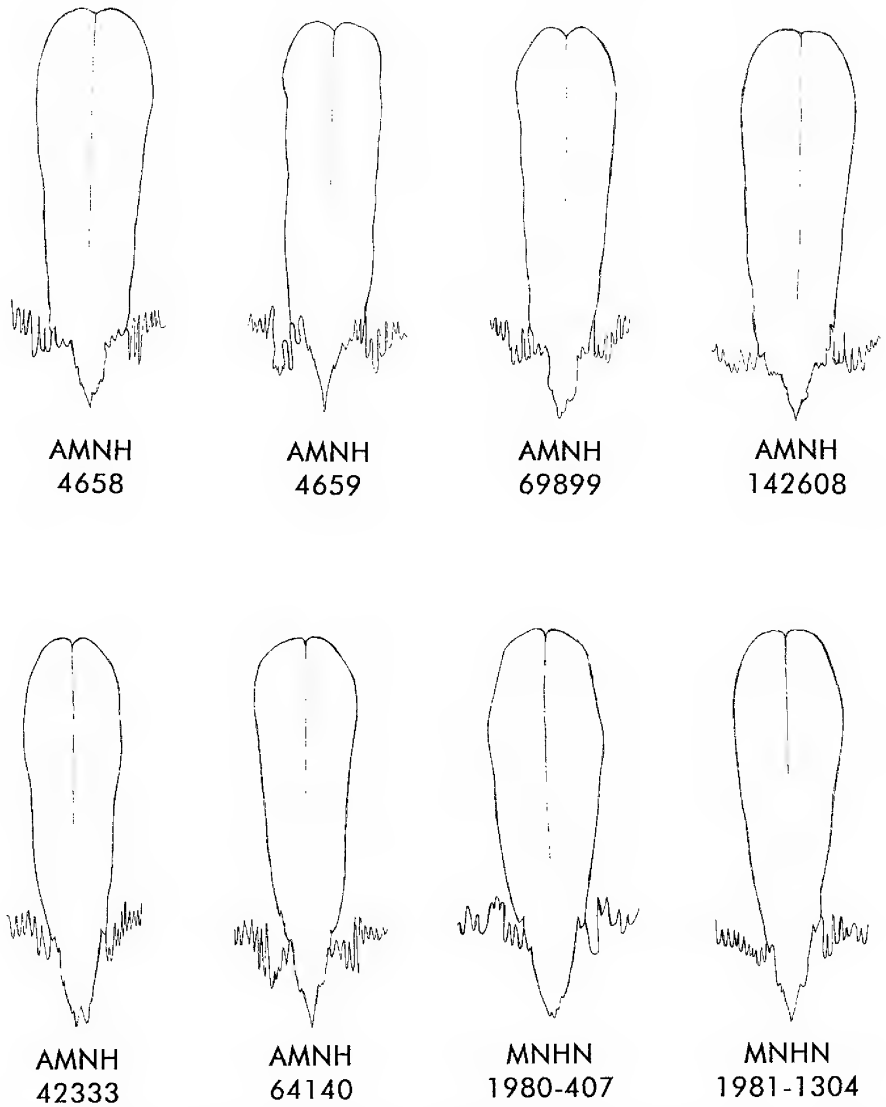

Fig. 44. Outlines of nasal bones in typical examples of *Nectomys palmipes* (top row) and *N. melanius* (bottom row). Whereas the nasals are abruptly constricted behind the premaxillary-frontal suture in *N. palmipes,* these bones are more-or-less evenly tapered throughout their length in *N. melanius.* Although atypical morphologies occur uncommonly in both species, this character is useful for taxonomic identifications when used in combination with other cranial traits (table 24; figs. 45–47).

scribed *N. parvipes* from French Guiana and compared it with sympatrically collected material that he identified as *N. s. melanius.* The identification of our voucher material therefore involves each of the three species of *Nectomys* regarded as valid by Musser and Carleton (1993).

All of the French Guianan material we examined agrees closely with the descriptions of *Nectomys squamipes melanius* provided by Thomas (1910), Hershkovitz (1944), and Husson (1978). The French Guianan holotype of *Nectomys parvipes,* raised in the laboratory from a wild-caught nestling (Petter, 1979), appears to be no more than an unusually small individual (table 23), perhaps stunted by an inadequate diet or other captive conditions. We examined this specimen (MNHN 1979.345) and determined that none of its qualitative characters diverge from the

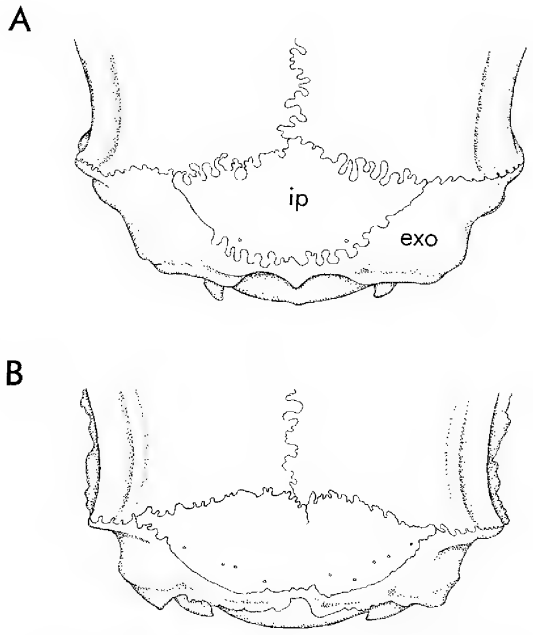

Fig. 45. Morphology of the occipital region in *Nectomys palmipes* (**A,** AMNH 4658 [holotype]) and *N. melanius* (**B,** MNHN 1981.1296). In *N. palmipes,* the interparietal (**ip**) is deep (anteroposterior dimension) relative to its width (transverse dimension), and the exoccipital (**exo**) occupies most of the dorsolateral surface of the occiput. By contrast, the interparietal of *N. melanius* is relatively much wider than deep, and the dorsolateral exposure of the exoccipital is correspondingly reduced.

range of variation exhibited by other specimens of French Guianan *Nectomys* with substantially larger measurements. Although the range of variation in molar length (LM) in our French Guianan series is considerable (5.9–7.1 mm), there is no hint of bimodality in the frequency distribution of this measurement, and there is no correlated variability in other characters to suggest that our sample is composite. French Guianan skins are not quite as dark, on average, as topotypical *melanius* from Guyana, but this appears to be the only point of external difference. Although measurements of Guyanese exemplars suggest that there may be a modest east-to-west increase in average molar size in this taxon (table 23), our side-by-side comparisons of French Guianan and Guyanese specimens revealed no qualitative craniodental differences. Based on specimens we examined, the same phenotype apparently extends westward into the Venezuelan state of Amazonas, and southward into the Brazilian state of Pará on the north bank of the Amazon.

We provisionally recognize *Nectomys melanius* as a distinct species based on geographical, morphological, and cytogenetic comparisons with both of the taxa that have previously been considered to be senior synonyms (table 24). From *N. palmipes,* its nearest neighbor, *melanius* differs conspicuously in diploid chromosome counts (2N = 16–17 versus 2N = 52–56; references in footnotes to table 24) and in several morphological traits that can be used to identify museum specimens unaccompanied by karyotypes. (1) Whereas the lateral margins of the nasal bones taper gradually from front to back in *melanius* without a sharp change in angle at the premaxillary-frontal suture, the nasals of *palmipes* are more abruptly constricted behind the premaxillae (fig. 44) in most of the specimens we examined.[12] (2) The interparietal bone is a shallow and wide element in *melanius* (fig. 45B) versus deeper and narrower in *palmipes* (fig. 45A), a difference that is correlated with a marked dorsolateral expansion of the exoccipital in the latter species. (3) The nasolacrimal capsules on the sides of the rostrum are mostly exposed to lateral view in *melanius* (fig. 46B), but these structures are partially concealed by the zygomatic plate in *palmipes* (fig. 46A). (4) The tegmen tympani is usually inconspicuous in *melanius* (fig. 47B), but a large anterior process of the tegmen tympani is always present in *palmipes* (fig. 47A).

Based on museum specimens that we sorted by these four morphological characters, *Nectomys palmipes* occurs throughout the island of Trinidad, where the type (AMNH 5928/4658) was collected at Princestown. This species also occurs on the adjacent Venezuelan mainland, from which we examined several specimens including the type of *Nectomys squamipes tatei* Hershkovitz (1948a). Collected at San Antonio in the Venezuelan

[12] In addition to the Trinidadian specimens listed in table 23 (footnote e), we examined AMNH 69899 (the holotype of *tatei*), AMNH 142608, and USNM 415009 from northeastern Venezuela.

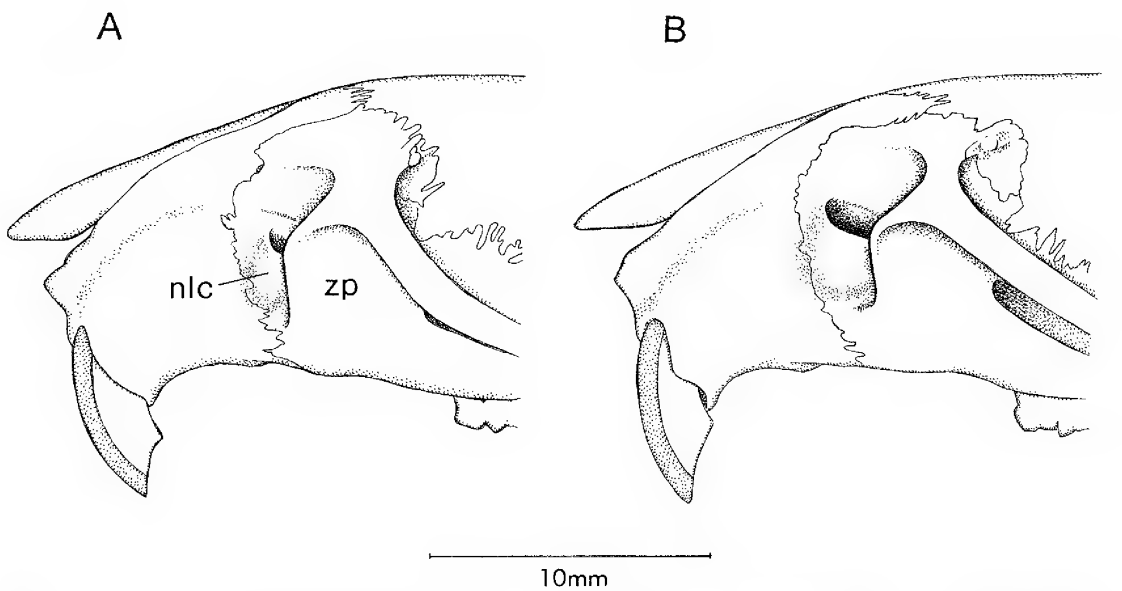

Fig. 46. Lateral views of the rostrum in *Nectomys palmipes* (**A,** AMNH 174241) and *N. melanius* (**B,** USNM 560824). In *N. palmipes,* the nasolacrimal capsule (**nlc**) is mostly obscured in lateral view by the very broad zygomatic plate (**zp**), but the nasolacrimal capsule is mostly exposed anterior to the narrower zygomatic plate of *N. melanius.*

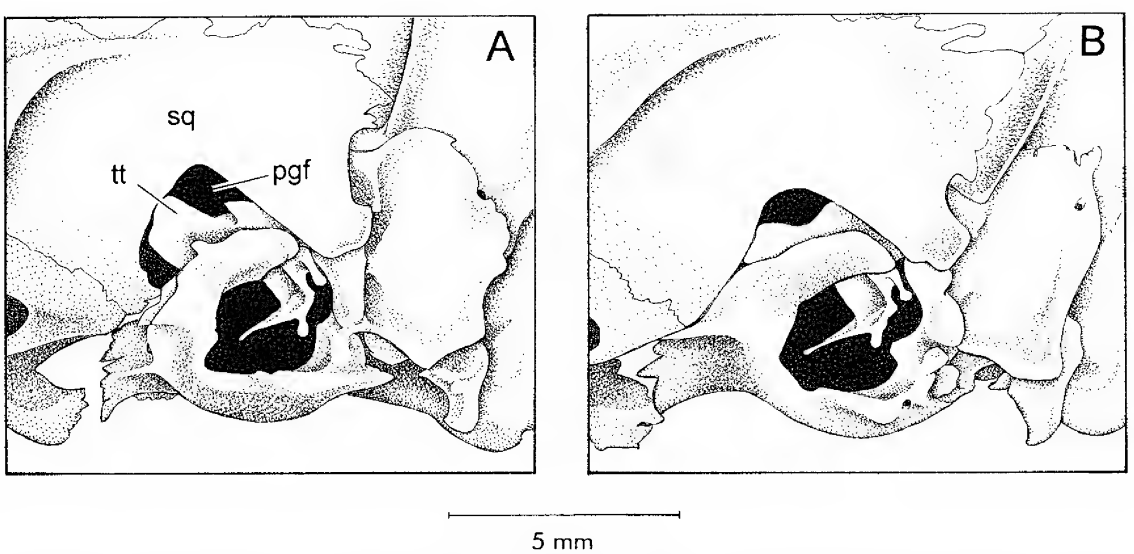

Fig. 47. Lateral view of the ear region in *Nectomys palmipes* (**A,** AMNH 235065) and *N. melanius* (**B,** USNM 406062). A large anterior process of the tegmen tympani (**tt**) that touches or overlaps the squamosal (**sq**) anterodorsal to the auditory bulla and anteroventral to the postglenoid foramen (**pgf**) is always present in *N. palmipes,* but the tegmen tympani is usually less exposed to lateral view in *N. melanius.*

TABLE 23
Measurements (mm) and Weights (g) of *Nectomys melanius* and *N. palmipes*

	melanius				
	French Guiana		Guyana		
	MNHN 1979.345[a]	Other specimens[b]	BMNH 6.4.8.32[c]	Other specimens[d]	*palmipes*[e]
Sex	female	13 males, 7 females	male	3 males, 5 females	14 males, 7 females, 1 unk.
HBL	135	185 ± 17 (135–205) 15	244	191 (173–210) 3	191 ± 23 (135–223) 19
LT	152	188 ± 15 (165–215) 14	200	191 (189–195) 3	189 ± 21 (135–219) 19
HF	38	46 ± 2 (42–50) 17	45	48 (46–51) 5	47 ± 3 (42–52) 11
Ear	17	20 ± 1 (17–22) 12	24	—	18 ± 3 (15–23) 9
CIL	—	37.6 ± 2.0 (33.5–40.5) 12	40.9	37.4 (35.0–40.7) 7	39.8 ± 3.0 (33.4–43.6) 22
LD	—	11.3 ± 0.8 (9.8–12.6) 16	11.6	11.2 (9.6–12.4) 7	11.8 ± 1.1 (9.4–13.2) 22
LM	5.9	6.4 ± 0.3 (5.9–7.1) 16	6.0	6.8 (6.6–7.0) 7	7.0 ± 0.2 (6.6–7.3) 22
BM1	2.0	2.0 ± 0.1 (1.9–2.2) 17	2.1	2.1 (1.9–2.2) 7	2.1 ± 0.1 (1.9–2.2) 22
LIF	—	7.4 ± 0.4 (6.8–8.3) 17	8.0	7.4 (6.7–8.3) 8	7.1 ± 0.5 (6.2–7.7) 22
BIF	—	3.4 ± 0.3 (2.8–4.0) 17	3.8	3.5 (2.8–4.1) 8	3.3 ± 0.3 (2.8–3.9) 22
BPB	3.4	4.1 ± 0.3 (3.4–4.7) 17	3.5	4.0 (3.6–4.4) 7	4.3 ± 0.5 (3.4–4.9) 22
BZP	3.7	4.4 ± 0.3 (3.9–4.8) 17	4.8	4.4 (3.9–4.7) 8	4.6 ± 0.4 (3.9–5.1) 22
LIB	6.1	7.0 ± 0.4 (6.3–7.6) 16	7.2	6.9 (6.6–7.4) 8	7.0 ± 0.4 (6.2–7.7) 22
ZB	19.3	21.8 ± 1.0 (19.7–22.8) 15	23.4	21.7 (19.9–23.3) 7	22.1 ± 1.4 (18.6–24.0) 22
Wt	—	180 (100–260) 4	—	—	197 (84–304) 9

[a] Holotype of *parvipes*, a very young captive-raised adult, consisting of a skin and partial skull.

[b] Including Paracou vouchers: MNHN 1970.224, 1980.407, 1981.162, 1981.164, 1981.184, 1981.1296–1981.1299, 1981.1303–1981.1305, 1986.270–1986.275, 1998.680, 1998.681.

[c] Holotype of *melanius*, an old adult; measurements courtesy of P. D. Jenkins.

[d] AMNH 34651, 42332, 42333, 42882, 42885, 42891, 64140; USNM 274567.

[e] All measured specimens are from Trinidad: AMNH 4658 (holotype of *palmipes*), 4659–4661, 4667, 6076, 6126, 169696, 169710, 169712, 169713, 173926, 174225, 174241, 186560, 186562, 186563, 235060–235063, 235065.

state of Monagas, the type of *tatei* (AMNH 69899) is craniodentally indistinguishable from Trinidadian material, as are two additional specimens from Monagas (AMNH 142608, USNM 415009); all were collected within the mapped distribution of karyotyped individuals with 2N = 16–17 chromosomes (in the states of Anzoategui, Delta Amacuro, Monagas, and Sucre; Barros et al., 1992). However, a single specimen with the same morphological characters (AMNH 16964) is from El Llagual (ca. 7°25′N, 65°10′W) in the northern part of Bolívar state. Because material from southern Bolívar (e.g., AMNH 75634, 75635, 130733, 130784) is unambiguously referable to *melanius,* specimens of water rats from intermediate localities in that state should be examined carefully to determine whether *melanius* and *palmipes* (the latter including *tatei* as a subjective junior synonym) are parapatrically or sympatrically distributed in eastern Venezuela.

Nectomys melanius closely resembles *N. squamipes* in all of the morphological traits by which *N. palmipes* differs from both (table 24), but we are persuaded by the karyotypic data and breeding experiments reported by Bonvincino et al. (1996), which suggest that the water rats of southeastern Brazil represent a distinct species from Amazonian populations. Based on the restricted type locality of *squamipes* (São Sebastião, São Paulo state; see Hershkovitz, 1944), this would appear to be the correct name for Bonvincino et al.'s southeastern Brazilian taxon. We agree with Patton et al. (2000) that *aquaticus* Lund (type locality: near Lagoa Santa, Minas Gerais) and *olivaceus* Hershkovitz (type locality: Therezopolis, Rio de Janeiro) are probable synonyms of *N. squamipes,* and that this species probably extends into northern Argentina. The observations of Peters (1861) and Hershkovitz (1944), together with our own examination of southeastern Brazilian

TABLE 24
Geographic, Morphological, and Karyotypic Comparisons among Three Species of *Nectomys*

	melanius[a]	*palmipes*[b]	*squamipes*[c]
Geographic range	Guiana subregion of Amazonia[d]	Trinidad and NE Venezuela	SE Brazil to NE Argentina
Plantar pads of pes[e]	usually five	five	usually six
Nasal margins	evenly tapering throughout	abruptly tapering behind premaxillae	variable
Interparietal ratio[f]	0.33 ± 0.04 (0.24–0.47) 38	0.47 ± 0.06 (0.39–0.63) 22	0.35 ± 0.04 (0.27–0.44) 20
Nasolacrimal capsules	mostly exposed in lateral view	partially concealed in lateral view	mostly exposed in lateral view
Tegmen tympani	usually with small anterior process	always with large anterior process	usually with small anterior process
Diploid number	2N = 52–56[g]	2N = 16–17[h]	2N = 55–59[i]

[a] Including *parvipes*.

[b] Including *tatei*.

[c] Probably including *olivaceus* and *aquaticus*, but types not seen.

[d] Possibly more widely distributed, but geographic limits unknown.

[e] Feet with five plantar pads are missing the lateral tarsal (hypothenar) pad.

[f] Depth (antero-posterior dimension) divided by width (transverse dimension). Tabulated statistics are the sample mean ± one standard deviation, the observed range (in parentheses), and the sample size. Measured specimens of *melanius* are listed in the text. Measured specimens of *palmipes* are listed in table 23 (footnote e). Measured specimens of *squamipes* are AMNH 61854–61859, AMNH 80397, and those tabulated by Hershkovitz (1944: tables II–IV).

[g] This report (six French Guianan specimens karyotyped by M. Tranier), Barros et al. (1992: two specimens from Amazonas federal territory, Venezuela), and Baker et al. (1983: six specimens from Surinam).

[h] Barros et al. (1992): one specimen from Trinidad and ten from northeastern Venezuela.

[i] Barros et al. (1992: two specimens from Misiones, Argentina) and Bonvincino et al. (1996: 58 specimens from southeastern Brazil).

material suggest that the hindfeet of *N. squamipes* usually have six plantar tubercles, whereas the hindfeet of most specimens of *N. melanius* lack a distinct hypothenar (lateral tarsal) pad.

Patton et al. (2000) used the name *apicalis* Peters (1861) for western Amazonian populations of *Nectomys* with low diploid numbers (2N = 38–42 chromosomes), large teeth (LM = 7.0–7.4 mm), and deep-narrow interparietals.[13] Based on the difference in diploid numbers alone, it seems unlikely that *apicalis* and *melanius* intergrade in western Amazonia (contra Hershkovitz, 1944: 51–52), but without having seen the type of *apicalis* and without undertaking an extensive analysis of morphological variation in western Amazonian populations of *Nectomys*, we are unable to rule out this possibility.

REMARKS: It seems probable that *Nectomys rattus*, originally described by Pelzeln (1883) based on a single immature specimen collected at Marabitanas (0°58′N, 66°51′W) on the upper Rio Negro in the Brazilian state of Amazonas, is a senior synonym of *melanius*. Although we have not seen Pelzeln's problematic type,[14] the geographic proximity of

[13] Barros et al. (1992) previously used the junior name *garleppi* Thomas (1899) for this form, and it is possible that other nominal taxa may also be synonyms.

[14] Thomas (1897: 497) remarked that the immature type of *Hesperomys rattus* Pelzeln "is clearly a *Nectomys*", but he did not explicitly state that he had seen the specimen. Tate (1939) apparently accepted Thomas's assignment of *rattus* to *Nectomys*, but Hershkovitz (1944: 30) objected on the grounds that Pelzeln's original description was not informative about generic characters: "Until the type itself, if still extant, can be examined, *Hesperomys rattus*, if at all identifiable, cannot be identified as a *Nectomys*." Although we have not seen the type, we did consult Thomas's manuscript notes (in the library of the Natural History Museum, London), which

Marabitanas to Venezuelan localities from which we have examined specimens referable to *melanius* tends to support this synonymy. Clearly, a comprehensive revision of *Nectomys* based on first-hand examination of relevant types and a critical analysis of morphological variation among the many hundreds of museum specimens now available for study will be essential for resolving this and other taxonomic enigmas. In the meantime, *N. melanius* is the oldest available name that we can confidently apply to the material at hand.

OTHER SPECIMENS EXAMINED: **Brazil**—*Pará,* Cachoeira Porteira (USNM 546290, 546291). **French Guiana**—Arataye (MNHN 1981.162), Awara (MNHN 1986.271), Cacao (MNHN 1979.345 [holotype of *parvipes*], 1981.1303, 1981.1304, 1986.272, 1986.273), Cayenne (MNHN 1970.224, 1981.1298, 1981.1299, 1986.274, 1986.275), Rorota (MNHN 1981.1305), Ouanary (MNHN 1981.1297), Piste St.-Élie (MNHN 1981.184), Saül (MNHN 1980.407, 1981.1296, 1986.270). **Guyana**—*Cuyuni-Mazaruni,* Kartabo (AMNH 42332, 42333, 42882, 42885, 42891, 64140), Oko Mountains (USNM 46216); *Upper Demerara-Berbice,* Rockstone (AMNH 34651). **Venezuela**—*Amazonas,* Acanaña (USNM 406237), Boca Mavaca (USNM 374662, 374664, 374665, 406062, 406063, 406233), Cerro Neblina Base Camp (USNM 560824), Esmeralda (AMNH 77303), Mt. Duida (AMNH 77306), Río Casiquiare (AMNH 78080), San Carlos de Río Negro (USNM 560650); *Bolívar,* Auyantepui (AMNH 130733, 130784), Mt. Roraima (AMNH 75634, 75635).

FIELD OBSERVATIONS: Both of our vouchers of *Nectomys melanius* were collected by O. Henry, whose field notes indicate that one was trapped "près de la crique" on 4 November 1989, and the other "sur la piste" on 20 April 1990.

include a bound volume of observations about the specimens he examined in European museums. Page 73 records his description of Pelzeln's type of *Hesperomys rattus* (in the NMW) as "a young . . . *Nectomys* . . . the toe webbing quite visible". Unfortunately, no other diagnostic characters were given, and we are not aware that anyone else has subsequently examined this specimen.

Neusticomys oyapocki (Dubost and Petter)
Figures 48, 49B, 49D

VOUCHER MATERIAL: AMNH 267597; MNHN 1995.992. Total = 2 specimens.

IDENTIFICATION: Our two vouchers and another specimen subsequently collected at nearby St.-Eugène provide an opportunity to reevaluate the characters of this obscure taxon. Previously known from a single specimen (MNHN 1977.775) from Trois Sauts in southeastern French Guiana, *Daptomys oyapocki* was initially diagnosed only by the absence of upper and lower third molars, and by the small size of its remaining cheekteeth (Dubost and Petter, 1978). Other distinctive attributes of the holotype were reported by Voss (1988), who treated *Daptomys* as a junior synonym of *Neusticomys.* The new material closely resembles the type and corroborates the status of *N. oyapocki* as a valid species.

The Paracou examples are both males. The smaller specimen (MNHN 1995.992) we judge to be subadult because of its uniformly blackish pelage, undescended testes, conspicuous metapodial epiphyses, and open basicranial sutures; although its molar dentition (see below) is completely erupted, the animal is obviously immature. The larger specimen (AMNH 267597; figs. 48, 49B, 49D) appears to be a young adult; its pelage is also dark, but the color is distinctly brownish and finely ticked with tawny-banded hairs, the testes are scrotal, the metapodial epiphyses are inconspicuous (but perhaps not completely absorbed), and the basicranial sutures are closed (although not completely fused). In fact, AMNH 267597 seems to be nearly the same age as the holotype and compares with it closely in external and cranial dimensions (table 25). The specimen from St.-Eugène is a fully adult male, with fur like the larger Paracou specimen, well-worn molars, and fused basicranial sutures.

Like the holotype, all of the three new specimens of *Neusticomys oyapocki* lack M3/m3, and the remaining molars are small by comparison with their homologs in the only other Guianan congener, *N. venezuelae* (fig. 49). As noted by Voss (1988), loss of the third molar is accompanied by morphological changes in the second, now the most poste-

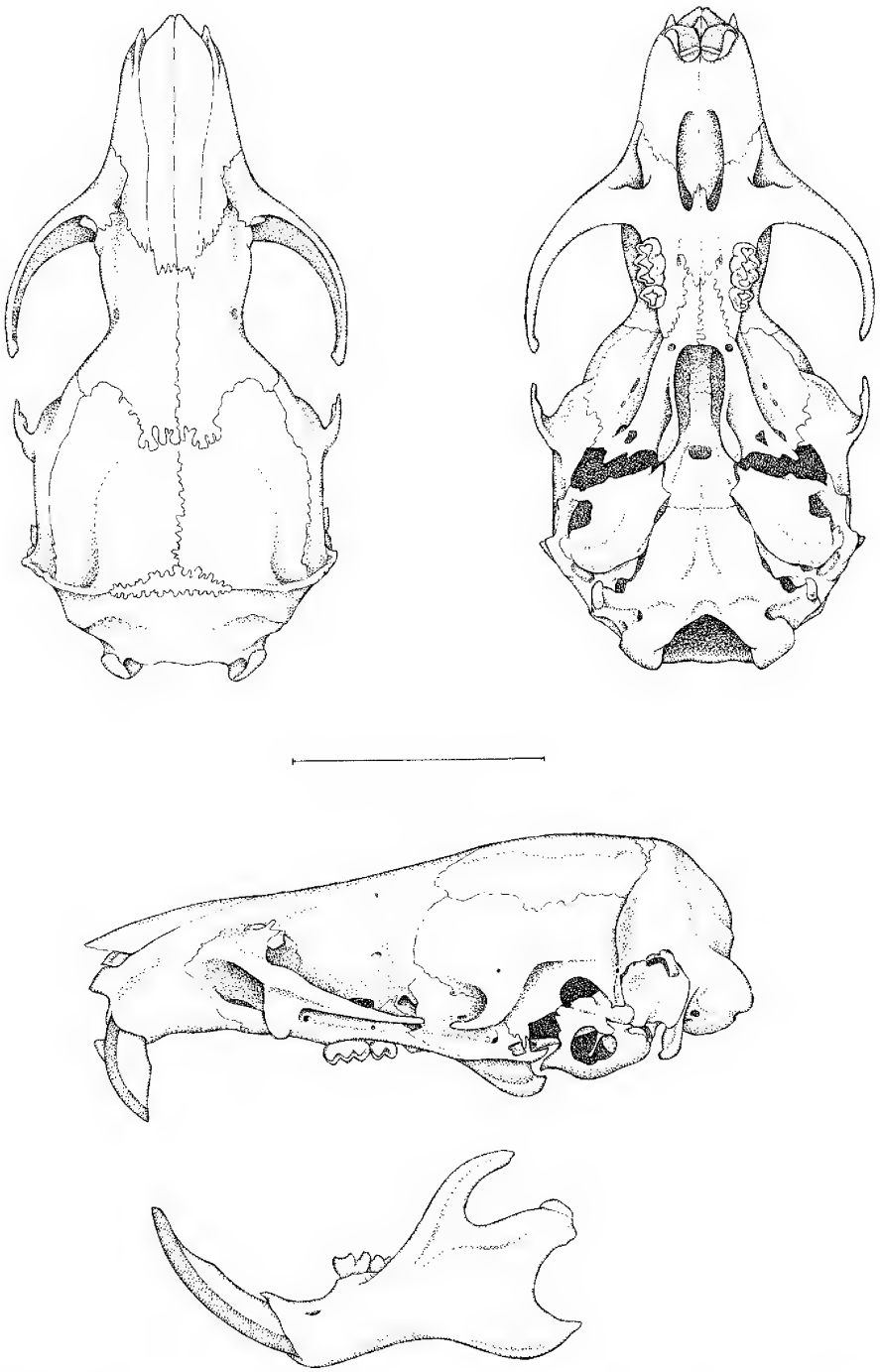

Fig. 48. Dorsal, ventral, and lateral views of the skull of *Neusticomys oyapocki* (AMNH 267597). Scale bar = 10 mm.

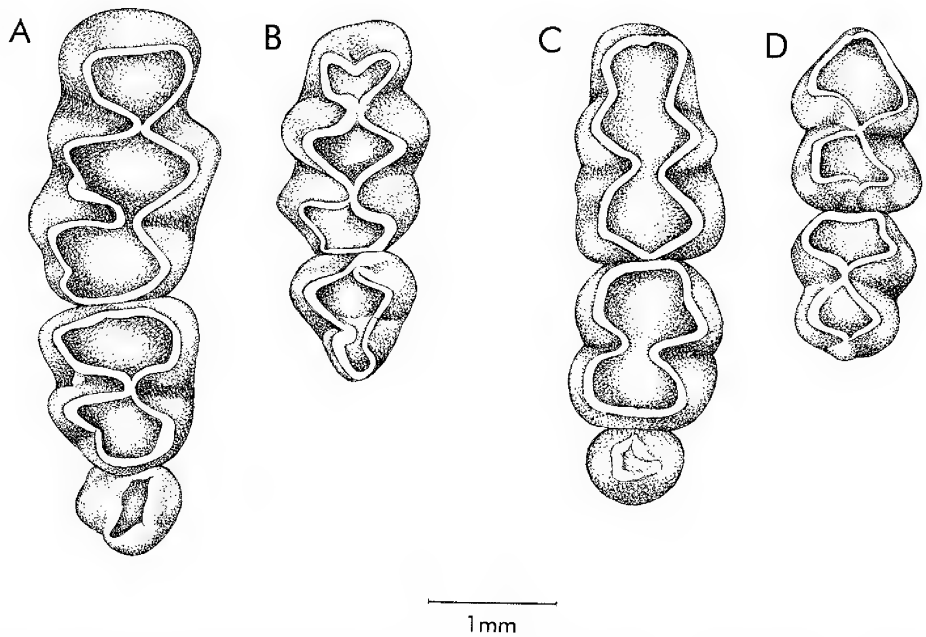

Fig. 49. Occlusal views of upper (**A, B**) and lower (**C, D**) molars of *Neusticomys venezuelae* (**A, C** [AMNH 69907, holotype]) and *N. oyapocki* (**B, D** [AMNH 267597]). Absence of upper and lower third molars conspicuously distinguishes *N. oyapocki* from *N. venezuelae*; the remaining cheekteeth of *N. oyapocki* are also absolutely smaller than their homologues in *N. venezuelae.* Additionally, the posterior lobe (metacone/hypocone cusp-pair) of M2 in *N. oyapocki* is greatly reduced relative to the anterior lobe (paracone/protocone) of that tooth, whereas the anterior and posterior lobes of M2 are subequal in *N. venezuelae.*

rior element in the toothrow. In all specimens of *N. oyapocki,* the hypocone/metacone lobe of M2 is greatly reduced by comparison with that of *N. venezuelae,* and there is no trace of a posteroloph.

Neusticomys oyapocki can be distinguished from other lowland congeners (formerly classified as *Daptomys*; fig. 50) by additional characters: (1) The ears and feet of *N. mussoi* and *N. peruviensis* are cream-colored and contrast with the brownish dorsal body pelage, but the ears and feet of *N. oyapocki* and *N. venezuelae* are dark brown and do not contrast with the dorsal fur. (2) In *N. venezuelae* and *N. mussoi,* the posterior edge of the inferior zygomatic root (zygomatic plate) lies above or just anterior to the anterocone of M1; in fully adult examples of *N. oyapocki* and *N. peruviensis,* however, the posterior edge of the inferior zygomatic root is located well anterior to the toothrow (fig. 48; also see illustrations in Musser and Gardner [1974], Voss [1988], and Ochoa and Soriano [1991]). (3) A small orbicular apophysis of the malleus is present on the type (and only known fully adult specimen) of *N. peruviensis,* but this structure is absent in both *N. oyapocki* and *N. venezuelae*; the character has not been described or illustrated for *N. mussoi.* Table 26 summarizes these and other relevant comparisons.

Two peculiarities of the holotype of *Neusticomys oyapocki* noted by Voss (1988) are apparently not diagnostic for the species. The type lacks masseteric tubercles, the bony processes from which M. masseter superficialis originates in ichthyomyines, but a distinct masseteric tubercle is present at the base of the inferior zygomatic root on each side of the skull in the larger Paracou specimen (AMNH 267597) and in MNHN 1995.3234 (from St.-Eugène). The type of *N. oyapocki* also appears to have an unusually narrow interorbital constriction by comparison with both of the other conspecific adults at hand,

TABLE 25
Measurements (mm) and Weights (g) of *Neusticomys oyapocki* and *N. venezuelae*

	oyapocki			*venezuelae*				
	MNHN 1977.775[a]	AMNH 267597	MNHN 1995.3234	AMNH 69907[b]	AMNH 69908	AMNH 257344	AMNH 257345	USNM 406123
Age[c]	2/o/a	2/c/a	3/f/a	2/o/i	2/o/i	3/c/a	4/f/a	3/f/a
Sex	male	male	male	male	female	female	male	female
HBL	114	112	110	131	112	132	120	100
LT	82	84	87	105	111	120	115	109
HF	26	25	24	28[d]	28[d]	27	26	25[d]
Ear	9[d]	10[d]	12	10[d]	11	13	12	10
CIL	27.2	26.3	27.9	26.9	26.9	28.6	—	26.0
LD	7.6	7.4	7.8	6.9	6.9	7.6	7.4	6.7
LM	—	—	—	4.1	4.2	3.9	4.1	4.0
M1–M2	3.0	3.0	2.9	3.4	3.6	3.3	3.5	3.3
BM1	1.1	1.1	1.1	1.3	1.4	1.4	1.4	1.3
LIF	5.2	4.6	4.8	4.8	4.8	5.6	—	5.2
BPB	3.0	2.7	2.8	2.7	2.5	2.6	—	2.7
BZP	1.5	1.4	1.5	1.1	1.2	1.5	1.3	1.3
LIB	4.8	5.4	5.4	5.2	5.3	5.3	5.1	5.0
ZB	13.7	13.8	15.1	13.3	12.8	—	—	13.7
Wt	47	43	—	—	—	66	58	

[a] Holotype of *oyapocki*.
[b] Holotype of *venezuelae*.
[c] Age criteria and notation after Voss (1988: 271–272).
[d] Remeasured from dried skin or fluid-preserved specimen.

and with specimens of *N. venezuelae* (table 25).

OTHER SPECIMENS EXAMINED: **French Guiana**—St.-Eugène (MNHN 1995.3234), Trois Sauts (MNHN 1977.775 [holotype]).

FIELD OBSERVATIONS: Both of our specimens of *Neusticomys oyapocki* from Paracou were taken in pitfall traplines in primary forest. The first example (AMNH 267597) was collected on 14 August 1993 about 5 m from a small (ca. 1.4 m wide), shallow (ca. 20 cm deep), clear, sandy-bottomed stream; the habitat at this site is perhaps best characterized as moist creekside forest on level sandy soil (fig. 51). The second animal (MNHN 1995.992) was taken on 8 September 1993 at approximately the same distance from a slightly smaller stream, but on sloping, well-drained ground. The remains of small crabs (fig. 52) found along other streams in our study area suggest that this species is not uncommon locally, but intensive trapping with Victors and Tomahawks set at streamside and baited with crabs produced no additional specimens.

Oecomys Thomas

For most of the last three decades, Neotropical mammalogists have identified small specimens of *Oecomys* (formerly considered a subgenus of *Oryzomys*) as *O. bicolor* and large specimens as *O. concolor* following Hershkovitz (1960). Unpublished revisionary research, however, suggests that at least 13 valid species of *Oecomys* are represented among the many nominal taxa that Hershkovitz lumped into *bicolor* and *concolor* (see Musser and Carleton, 1993). Four morphologically diagnosable species are known to occur in French Guiana (table 27), of which two are represented among our vouchers. Pending the publication of a comprehensive revision of this difficult genus, we offer preliminary descriptions and diagnostic comparisons of both Paracou species to document our identifications.

Species of *Oecomys* are small to medium-sized murids, ranging in average adult body weight from about 20 to 60 g. The dorsal fur is soft (not spiny) and, in adults with fresh

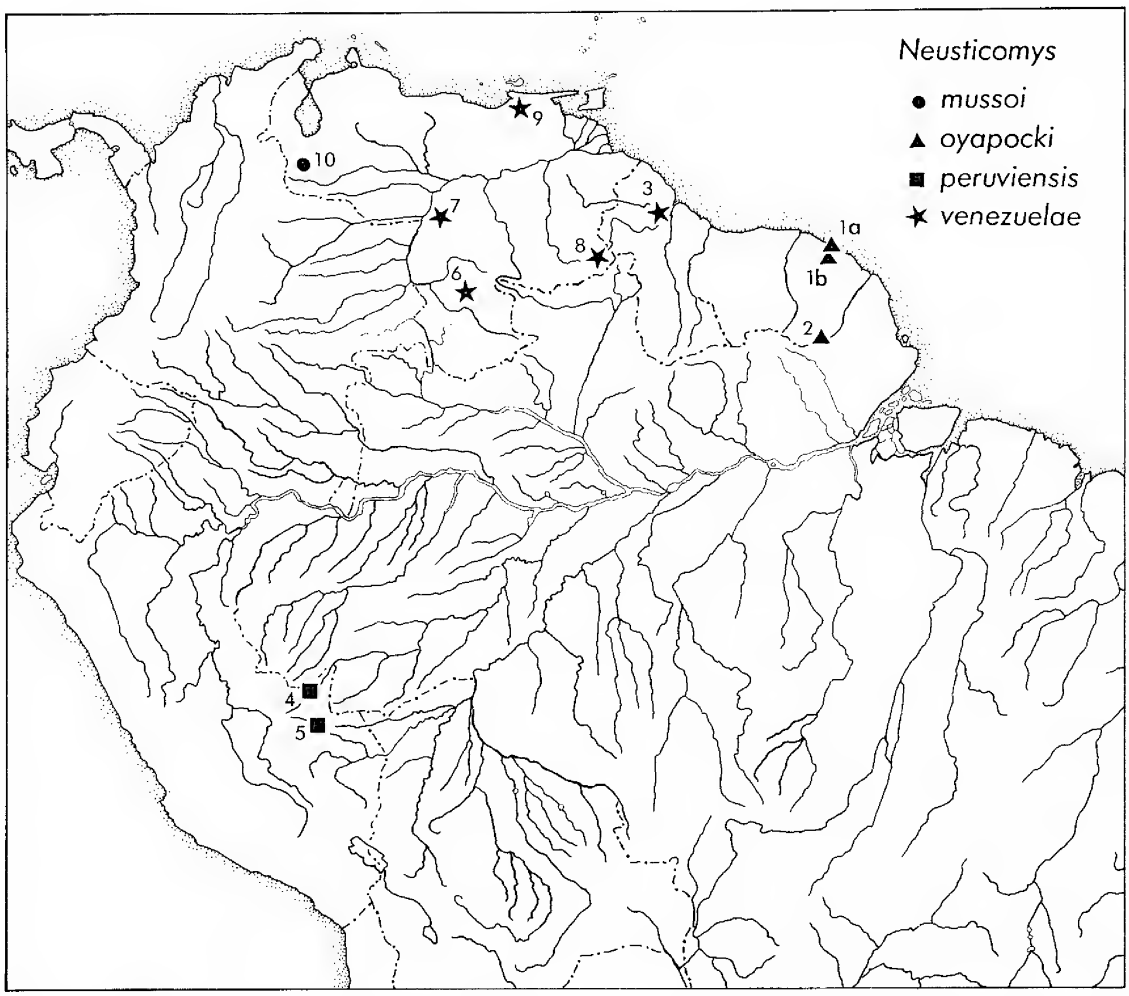

Fig. 50. Known collection localities of lowland species of *Neusticomys* based on specimens examined and the literature (see citations in footnotes to table 26). **1a,** FRENCH GUIANA, Paracou; **1b,** FRENCH GUIANA, St.-Eugène; **2,** FRENCH GUIANA, Trois Sauts; **3,** GUYANA, *Cuyuni-Mazaruni,* Kartabo; **4,** PERU, *Ucayali,* Balta; **5,** PERU, *Madre de Dios,* Pakitza; **6,** VENEZUELA, *Amazonas,* Cerro Duida; **7,** VENEZUELA, *Bolívar,* Los Pijiguaos; **8,** VENEZUELA, *Bolívar,* San Ignacio Yuruaní; **9,** VENEZUELA, *Sucre,* Río Neverí; **10,** VENEZUELA, *Táchira,* 14 km SE Pregonero.

pelage, usually some shade of reddish brown. The ventral fur can be either self-colored (pure white) or gray-based with a superficial wash of white, buff, or orange. The mystacial vibrissae are long, extending well behind the pinnae when laid back alongside the head. The dorsal pelage of the hindfeet is sometimes indistinctly darker over the metatarsals than on the digits, but sharply defined metatarsal spots or bands are absent; the plantar surface of the hindfoot is either unpigmented (whitish in preservative, pink in life, brown or amber in dried skins) or lightly pigmented (grayish), but apparently never blackish. Structurally, the hindfeet are short and broad, with large plantar pads and semi-opposable fifth digits (fig. 53B). Tails are unicolored in most species (dark above and below), and they are usually longer than the combined length of head-and-body; a terminal tuft of long hairs is present in some, but not all species.

Amazonian species of *Oryzomys* are sometimes misidentified in the field as *Oecomys*

TABLE 26
Geographic and Morphological Comparisons among Lowland Species of *Neusticomys*

	mussoi[a]	*oyapocki*[b]	*peruviensis*[c]	*venezuelae*[d]
Known distribution	W Venezuela	French Guiana	E Peru	Guyana, E and S Venezuela
Fur of ears and feet	pale	dark	pale	dark
Third molars	present	absent	present	present
LM (observed range)	3.3–3.4 mm	—	3.8–4.0 mm	3.8–4.3 mm
Inferior zygomatic root	near M1	anterior to M1	anterior to M1	near M1
Orbicular apophysis[e]	?	absent	small	absent

[a] Two specimens are known from a single locality (Ochoa and Soriano, 1991).

[b] Four specimens are known from three localities (Dubost and Petter, 1978; this report).

[c] Two specimens are known from two localities (Musser and Gardner, 1974; Pacheco and Vivar, 1996). The qualitative characters tabulated are those of the holotype (LSU 14407), a fully adult specimen. The younger example described by Pacheco and Vivar appears to have immature pelage and differs in cranial characters that may be age-related.

[d] Eleven specimens are known from five localities (Voss, 1988, 1991: table 23; Ochoa and Soriano, 1991).

[e] Of the malleus (see Voss, 1988: 299, fig. 20).

(and vice versa), but differ externally by their much shorter mystacial vibrissae (not extending behind the pinnae), distinctive hindfeet (fig. 53A), and shorter tails that are often bicolored (at least basally) and never have terminal tufts of long hairs (see the account of *Oryzomys* below for more detailed descriptions of external traits).

Species of *Rhipidomys* resemble *Oecomys* externally in possessing long mystacial vibrissae; short-broad hindfeet with unpigmented soles, large plantar pads, and semiopposable fifth digits; and long, usually unicolored, tufted tails. However, the hindfeet of *Rhipidomys* are distinctive, with darker metatarsal markings, larger plantar pads, and relatively longer fifth pedal digits (fig. 53C). In addition, whereas female *Oecomys* have eight mammae, female *Rhipidomys* have only six. More detailed comparisons between like-sized species of *Oecomys* and *Rhipidomys* that might be confused in the field are provided in the account that follows.

Oecomys auyantepui Tate

Figures 53B, 55, 56, 57A, 62B

VOUCHER MATERIAL: AMNH 266560, 266564, 267593, 267595, 267596; MNHN 1995.1027, 1995.1028. Total = 7 specimens.

IDENTIFICATION: *Oecomys auyantepui* was originally described by Tate (1939) from two specimens collected at 1100 m elevation on Auyantepui in Estado Bolívar, Venezuela. Hitherto regarded as a junior synonym of *O. concolor* (by Hershkovitz, 1960), *O. trinitatis* (by Cabrera, 1961), or *O. paricola* (by Musser and Carleton, 1993), *auyantepui* is unambiguously diagnosable from other named forms of *Oecomys* and merits recognition as a distinct species. Distinguishing traits include its predominantly gray-based ventral fur, a distinctly tufted tail, lack of broadly shelved supraorbital margins and postorbital processes, a primitive carotid arterial circulation, presence of an alisphenoid strut, a large postglenoid foramen, complete closure of the subsquamosal fenestra, and a distinctive range of morphometric variation (see table 27 and below). All of the specimens we refer to *O. auyantepui* are from the Guiana subregion of Amazonia (fig. 54).

In the hand, *Oecomys auyantepui* is an attractive mouse with soft reddish-brown fur that is much brighter in mature adults with fresh glossy pelage than in juveniles, subadults, or specimens with obviously worn, dull coats. The small ears are covered with a short but macroscopically visible pelage that is colored essentially like that of the head and nape (not contrastingly darker). The ventral fur, superficially whitish, cream-colored, or pale buff, is sharply set off from the reddish-brown fur of the sides and back. The ventral fur is predominantly gray-based in

Fig. 51. Pitfall trapline that captured *Neusticomys oyapocki* in creekside primary forest at Paracou. This trapline roughly paralleled the small stream illustrated in figure 9, which was only about 10 m to the right of this view.

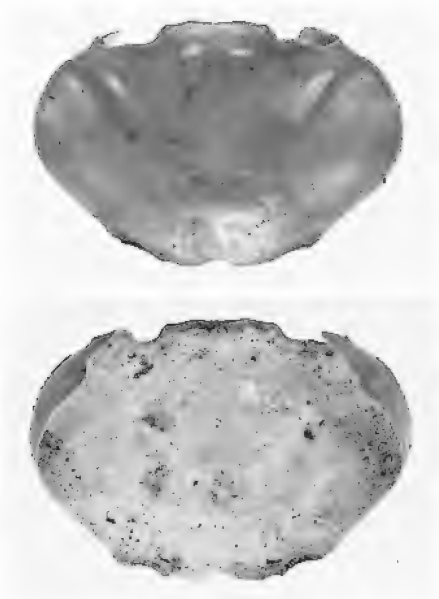

Fig. 52. Dorsal and ventral views of one of several pseudothelphusid crab carapaces found near small streams at Paracou. Patterns of breakage along the posterior and ventrolateral margins of this example match those observed on the carapaces of like-sized pseudothelphusids eaten by captive ichthyomyines (Voss et al., 1982: fig. 3). Such remains provided the first evidence that ichthyomyines were resident in our study area, an inference subsequently confirmed by trapped specimens of *Neusticomys oyapocki*. Both views about 2×.

most of the specimens at hand, but the fur of the chin and throat is usually self-colored (all pale), and a few specimens have self-colored fur extending caudally along the ventral midline to the groin. The hindfeet are either covered uniformly with pale buffy hairs or the metatarsus is indistinctly darker than the toes, but a distinct metatarsal band of blackish fur is apparently never present. Undamaged tails are uniformly dark (almost blackish in some specimens) with a terminal tuft of hairs that are distinctly longer (6–10 mm) than the short (<2 mm) hairs on the proximal part of that organ.

The skull (figs. 55, 56) is unremarkable in general aspect, with the short rostrum, shallow zygomatic notches, convergent interorbit, beaded supraorbital margins, wide-long palate, and small bullae characteristic of this oryzomyine genus. The incisive foramina are of average length relative to the diastema (neither very short nor very long by oryzomyine standards), with wide and more-or-less evenly convex lateral margins. The roof of the mesopterygoid fossa is completely bony, with no trace of sphenopalatine perforations in most of the specimens at hand. A large stapedial foramen on the medial surface of the bulla, a translucent squamosal-alisphenoid groove on the internal surface of the braincase, and a distinct sphenofrontal foramen in the rear of the orbit indicate that the pattern of carotid arterial supply is primitive (pattern 1 of Voss, 1988). A robust diagonal strut of the alisphenoid bone separates the foramen ovale accessorius from the buccinator-masticatory foramen on both sides of the skull in most specimens, and the subsquamosal fenestra is invariably absent (fig. 57A; see table 29).

Morphometrically, series of *Oecomys auyantepui* that we measured from Guyana, French Guiana, and Brazil (Amapá) are remarkably similar (table 28). In fact, the most divergent specimen we examined is the Venezuelan type (AMNH 131156), which is larger than most of the other material at hand but does not differ in any qualitative external or craniodental character. Additional Venezuelan material would be useful to determine whether the type represents a western population characterized by large size, or is merely an unusually large individual.

Oecomys auyantepui is intermediate in size to other congeneric species that occur in the Guiana subregion of Amazonia, two of which (*O. bicolor* and *O. rutilus*) are substantially smaller, and four of which (*O. concolor, O. rex, O. roberti, O. trinitatis*) are larger. Additionally, other Guianan subregion species differ from *auyantepui* by having entirely self-colored (pure white) ventral fur (*bicolor, rutilus*), untufted tails (*concolor, rex, roberti, trinitatis*), more-or-less bicolored tails (*trinitatis*), broadly shelved supraorbital margins (*rex*), a derived pattern of carotid arterial supply (*concolor*), confluent accessory oval and buccinator-masticatory foramina (most *bicolor* specimens), and/or patent subsquamosal fenestrae (*bicolor, concolor, rutilus, trinitatis*). Instead, *Oecomys auyantepui* is morphologically most similar

TABLE 27

Diagnostic Morphological Comparisons among French Guianan Species of *Oecomys*

(Tabulated data include information from specimens collected throughout the Guiana subregion of Amazonia.)

	rex[a]	*auyantepui*[b]	*bicolor*[c]	*rutilus*[b]
External characters				
Length of hindfoot[d]	29 ± 1 mm (27–31 mm) 13	24 ± 1 mm (23–27 mm) 36	22 ± 1 mm (21–23 mm) 15	21 ± 1 mm (19–22 mm) 32
Dorsal fur length[e]	11–14 mm	8–11 mm	4–5 mm	6–8 mm
Ventral fur color	uniformly gray-based	mostly gray-based, but often w/ middorsal streak of pure white	pure white[f]	pure white[f]
Terminal tail tuft[e]	absent (≤2 mm)	present (6–10 mm)	present (4–5 mm)	present (6–10 mm)
Craniodental characters				
Length of upper molars[d]	5.4 ± 0.2 mm (5.2–5.7 mm) 12	4.1 ± 0.1 mm (3.8–4.5 mm) 42	3.7 ± 0.1 mm (3.5–3.9 mm) 35	3.3 ± 0.1 mm (3.0–3.5 mm) 31
Interorbital morphology	shelved, w/ large postorbital processes	beaded, w/o processes	beaded, w/o processes	beaded, w/o processes
Alisphenoid strut	present or absent	usually present	usually absent	usually present
Subsquamosal foramen	very small or absent	always absent	always present	always present

[a] Specimens examined: AMNH 41908, 142806; BMNH 10.9.29.17 (holotype); MNHN 1982.621, 1983.386–1983.390; USNM 394254–394256, 399622; and an uncatalogued specimen from INPA with field number DIM 58.

[b] See text for specimens examined (includes Paracou vouchers).

[c] See text footnote 16 for specimens examined.

[d] Tabulated statistics include the sample mean ± one standard deviation, the observed mean (in parentheses), and the sample size.

[e] Typical range of variation.

[f] Rarely with indistinct gray hair bases or narrow lateral zones of gray-based fur.

to *O. paricola,* a species that we do not recognize as occurring in the Guiana subregion.

Oecomys paricola (Thomas, 1904) was originally described on the basis of a very young female specimen (BMNH 4.7.4.63) collected at "Igarapé-Assu" (= Igarapé Açu at 1°07′S, 47°37′W; Paynter and Traylor, 1991) near Belém. To evaluate the hypothesis that *O. paricola* and *O. auyantepui* are synonyms (Musser and Carleton, 1993), we examined the type of *paricola* and 21 additional specimens collected in the same interfluvial region (south of the Amazon and east of the Rio Tocantins).[15] Because it was not our intention to evaluate the taxonomic status of all museum material currently identified as *O. paricola,* we did not include specimens so determined from other interfluvial regions, some of which exhibit characters not shown by the type.

Oecomys paricola is about the same size as *O. auyantepui,* and these two species are perhaps indistinguishable in pelage color and external morphology. Cranially, however, two qualitative characters (table 29, fig. 57) permit unambiguous identification. (1) A well-developed alisphenoid strut almost always separates the buccinator-masticatory and accessory oval foramina in *auyantepui,* but an alisphenoid strut is missing and these foramina are consistently confluent in *paricola.* (2) Whereas the subsquamosal fenestra is consistently absent in *auyantepui,* a distinct subsquamosal fenestra (separated from the postglenoid foramen by the hamular process of the squamosal bone) is always pre-

[15] We examined specimens of *Oecomys paricola* from the following localities: **Brazil**—*Pará,* Belem (USNM 393819, 393842, 461386, 545232, 545233), Capim (AMNH 188963, 203391, 203392, 203397; USNM 461385, 461388–461395, 461400), Igarapé Açu (BMNH 4.7.4.63, 4.7.4.64, 4.7.4 108).

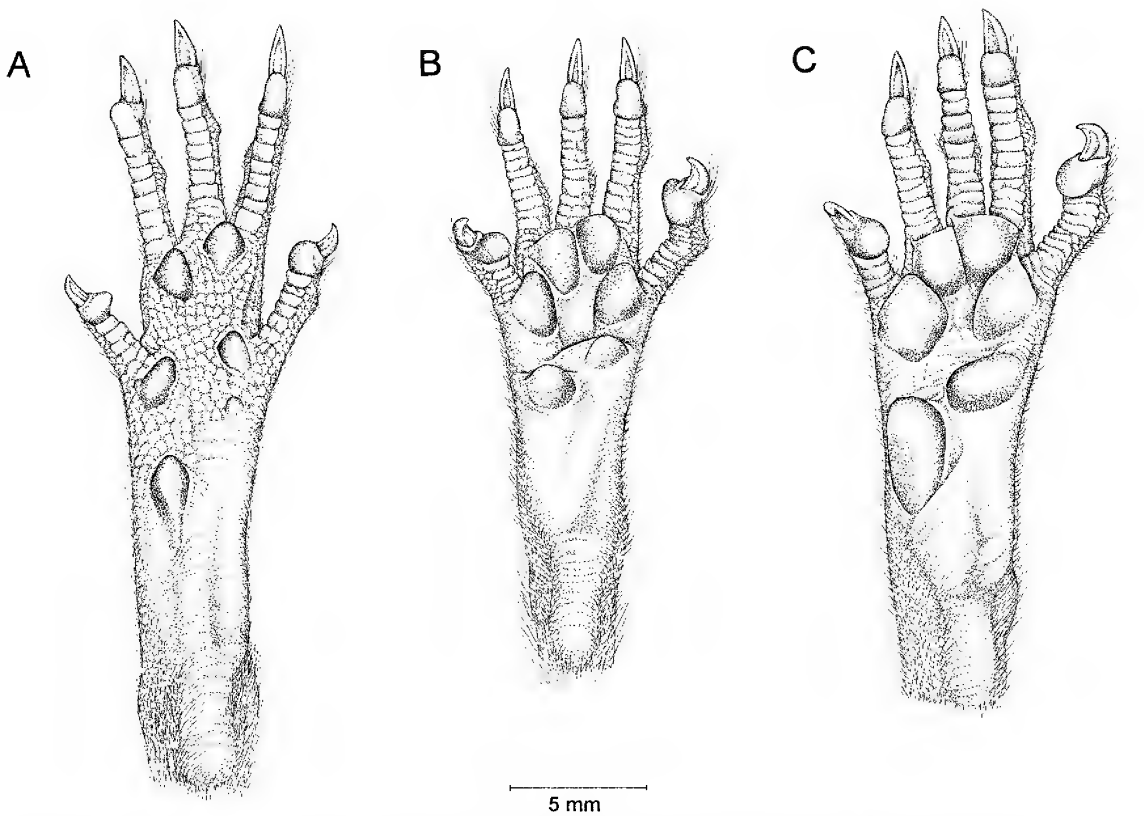

Fig. 53. Plantar views of left hindfeet of *Oryzomys megacephalus* (**A,** AMNH 266527), *Oecomys auyantepui* (**B,** AMNH 267595), and *Rhipidomys nitela* (**C,** AMNH 267583) illustrating diagnostic intergeneric differences. The hindfeet of Amazonian species of *Oryzomys* are proportionately narrow; the three central digits (II, III, and IV) are conspicuously longer than the outer digits (I and V); digit V is not opposable; the plantar epithelium is at least partially pigmented (grayish in fresh material); the plantar pads are small, hard, and more-or-less conical; and the skin between the pads is studded with small, scale-like tubercles. By contrast, the hindfeet of *Oecomys* and *Rhipidomys* are proportionately broader; digits I and V are longer relative to II–IV; digit V is semi-opposable; the plantar epithelium is usually entirely unpigmented (pinkish in fresh material); the plantar pads are larger, softer, cushion-like structures; and the skin between the plantar pads is smooth or creased but never tuberculate. Despite differences in hindfoot size and other features between the illustrated examples of *O. auyantepui* and *R. nitela,* their respective genera do not seem to be consistently distinguishable by pedal morphology.

sent in *paricola.* Although their close resemblance in other respects suggest that *auyantepui* and *paricola* are likely to be sister taxa, we recognize them as valid (diagnosable) species allopatrically distributed north and south of the Amazon.

Other Specimens Examined: **Brazil**—*Amapá,* Serra do Navio (USNM 393820, 393821, 394239–394243, 394246–394249, 461521); *Amazonas,* 80 km N Manaus (USNM 579996–580001). **French Guiana**—Arataye (MNHN 1986.865; USNM 578015, 578019), Iracoubo (1983.394, 1983.395), St.-Eugène (1994.124, 1995.3235, 1998.1844), Trois Sauts (MNHN 1983.398). **Guyana**—*Cuyuni-Mazaruni,* Kartabo (AMNH 64135); *Potaro-Siparuni,* 5 km SE Surama (ROM 102944, 103051, 103052, 103244, 103288); *Upper Demerara-Berbice,* 18 km SW Kwakwani (AMNH 269829, 269830), Tropenbos (ROM 103433, 103502). **Venezuela**—*Bolívar,* Auyantepui (AMNH 131108, 131156 [holotype]).

Field Observations: All of our definite records of *Oecomys auyantepui* from Paracou are based on collected specimens. Of

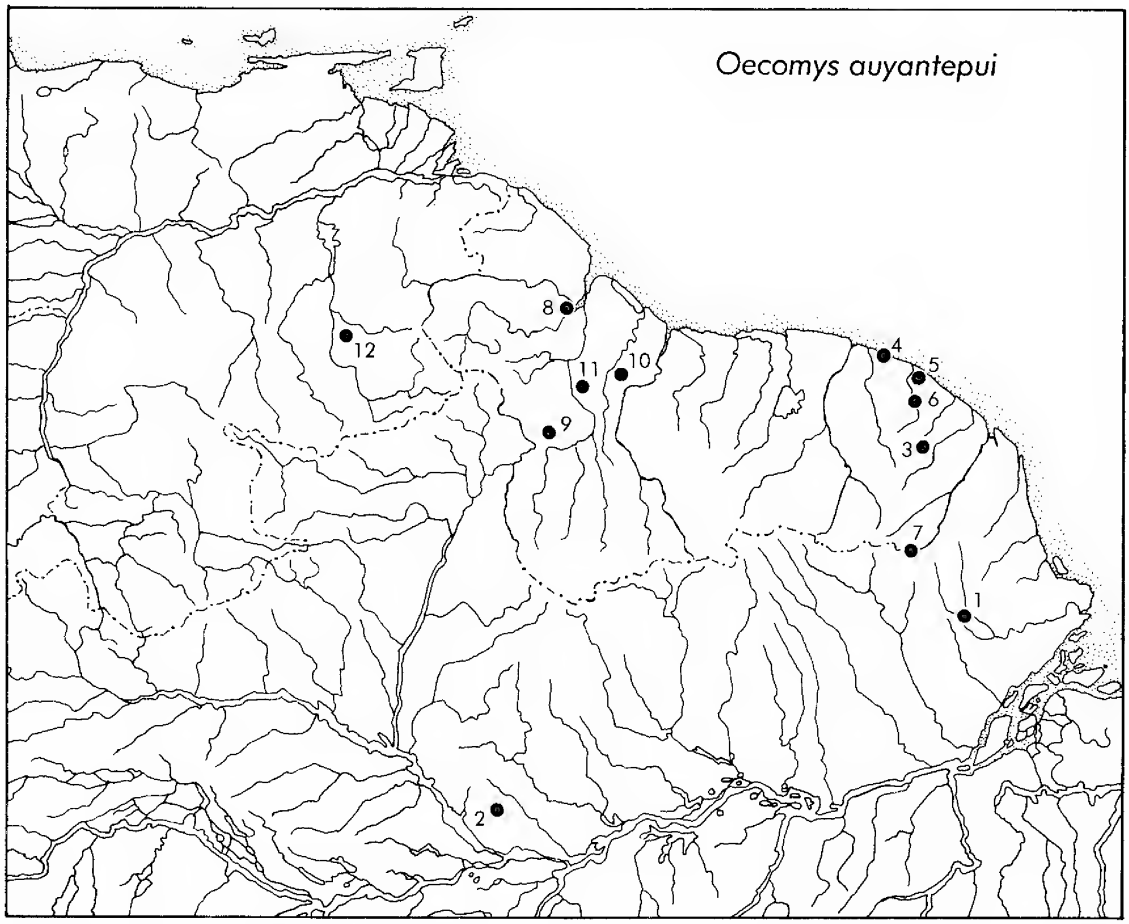

Fig. 54. Known collection localities for *Oecomys auyantepui* based on specimens examined. **1,** BRAZIL, *Amapá,* Serra do Navio; **2,** BRAZIL, *Amazonas,* 80 km N Manaus; **3,** FRENCH GUIANA, Arataye; **4,** FRENCH GUIANA, Iracoubo; **5,** FRENCH GUIANA, Paracou; **6,** FRENCH GUIANA, St.-Eugène; **7,** FRENCH GUIANA, Trois Sauts; **8,** GUYANA, *Cuyuni-Mazaruni,* Kartabo; **9,** GUYANA, *Potaro-Siparuni,* 5 km SE Surama; **10,** GUYANA, *Upper Demerara-Berbice,* 18 km SE Kwakwani; **11,** GUYANA, *Upper Demerara-Berbice,* Tropenbos; **12,** VENEZUELA, *Bolívar,* Auyan-tepui.

these, one was taken on the ground in a Sherman trap, three were taken in Victor snap traps tied to lianas 1.2–1.5 m above the ground (fig. 58), and three were taken in arboreal platform traps 7.2–10.5 m above the ground. Three specimens were trapped in creekside primary forest, two in well-drained primary forest, and two in swampy primary forest. All specimens were found in the traps at or soon after dawn.

Oecomys rutilus Anthony

Figures 55, 56

VOUCHERS: AMNH 266561, 267584, 267586, 267588–267591, 269121; MNHN 1995.1023–1995.1026. Total = 12 specimens.

IDENTIFICATION: *Oecomys rutilus* was originally described by Anthony (1921b) based on a single specimen collected by W. Beebe at Kartabo, Cuyuni-Mazaruni District, Guyana. Anthony (p. 4) characterized *rutilus* as "A small, brightly colored species, with very short tail and clear white under parts", and he remarked that it was quite distinct from another species originally described from Guyana, *Oecomys nitedulus* Thomas (1910):

> Compared with *Oecomys nitedulus,* collected at the same place, *rutilus* is somewhat smaller superficially,

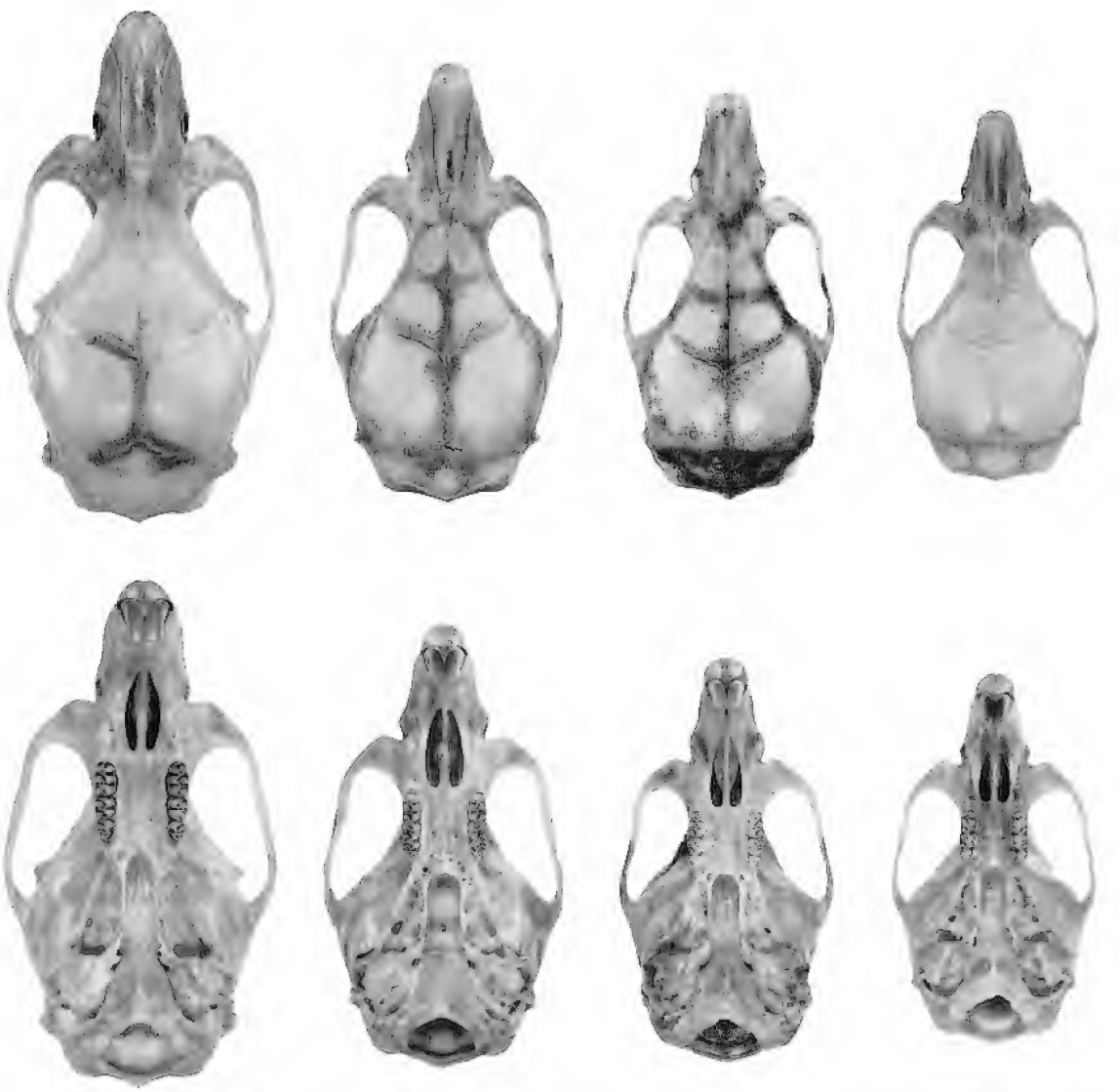

Fig. 55. Dorsal and ventral cranial views of four species of *Oecomys* from French Guiana. Left to right: *Oecomys rex* (DIM 58); *O. auyantepui* (USNM 578015); *O. bicolor* (USNM 394252); *O. rutilus* (AMNH 267589). All views about ×2.

much brighter in color, with longer, softer, pelage, shorter tail and conspicuously smaller skull.

Despite Anthony's explicit statement that *rutilus* and *nitedulus* were valid sympatric species, Hershkovitz (1960) listed both names as synonyms of *Oecomys bicolor,* a taxon originally described (Tomes, 1860) from eastern Ecuador. Hershkovitz (p. 539) admitted that he had not seen Anthony's type of *rutilus,* but remarked that "Judged by the original description, it is a subadult of the same Kartabo series identified by Anthony as *nitedulus.*"

Oecomys rutilus was listed as a valid species by Musser and Carleton (1993), but no account of its diagnostic characteristics has yet been published to supplement Anthony's preliminary observations. To identify our Paracou material, we examined every available specimen of small *Oecomys* from the Guiana subregion of Amazonia, including the types of *rutilus* and *nitedulus.* In the fol-

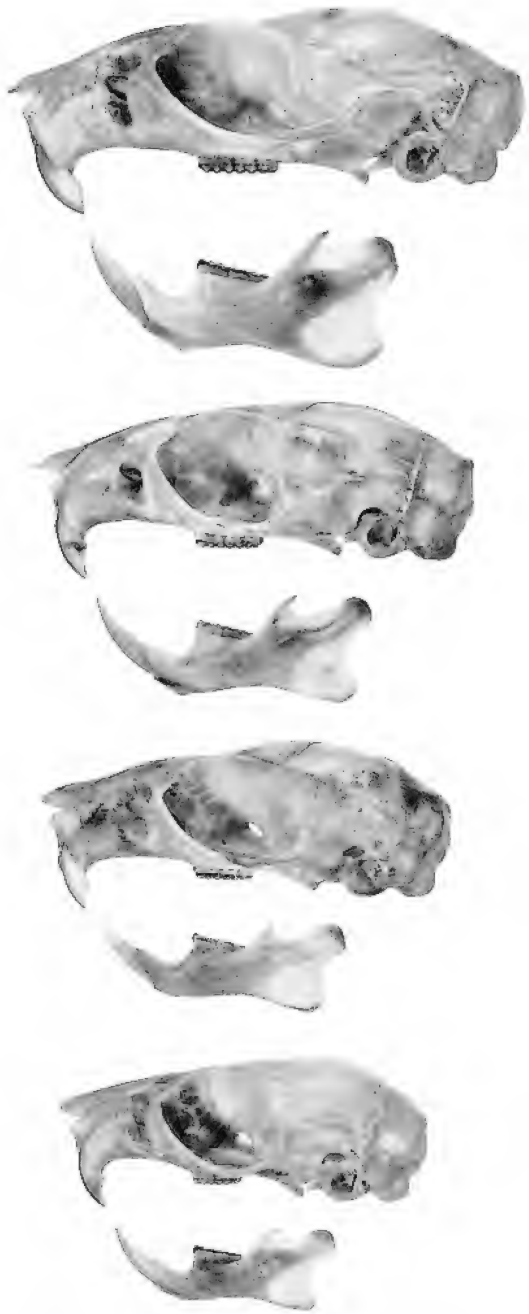

Fig. 56. Lateral cranial and mandibular views of four species of *Oecomys* from French Guiana. Top to Bottom: *Oecomys rex* (DIM 58); *O. auyantepui* (USNM 578015); *O. bicolor* (USNM 394252); *O. rutilus* (AMNH 267589). All views about ×2.5.

lowing account we provisionally accept the hypothesis that *nitedulus* and *bicolor* are conspecific (Hershkovitz, 1960; Musser and Carleton, 1993), but we note that this synonymy remains untested by published analyses of character data, and that we have not made a careful study of typical *bicolor* (from eastern Ecuador). Instead, our taxonomic comparisons are based exclusively on Guianan material.[16]

The frequency distribution of the length of the upper molar row (LM) for small *Oecomys* collected in the Guiana subregion of Amazonia (N = 66) is distinctly bimodal (fig. 59), with one peak in the interval 3.2–3.4 mm (including the type of *rutilus* with LM = 3.26 mm) and another in the interval 3.6–3.9 mm (including the type of *nitedulus* with LM = 3.79 mm). Although this univariate graph does not of itself show any morphometric discontinuity that could be used to sort specimens into discrete size classes (all frequency intervals between 3.0 and 4.0 mm are occupied), the bimodal pattern clearly indicates that our sample is heterogeneous. Fortunately, variation in other characters is correlated with molar toothrow length and provides unambiguous evidence for species diagnosis. In fact, the specimens we measured of the smaller species, *O. rutilus,* have molar toothrows shorter than 3.5 mm, whereas our measured specimens of *O. bicolor* have toothrows longer than 3.5 mm. With larger samples of both species, however, it seems inevitable that the observed ranges of variation in this dimension will eventually be found to overlap.

Oecomys rutilus and Guianan specimens of *O. bicolor* (= *nitedulus*) are similar in external appearance: both are small, usually reddish mice with dark, tufted tails and pure white venters (table 27). Although *rutilus* averages smaller than *bicolor* in all standard

[16] We examined specimens of *Oecomys bicolor* from the following localities: **Brazil**—*Amapá,* Serra do Navio (USNM 393822–393830, 393833–393839, 393843, 394251–394253, 461522). **French Guiana**—Les Nouragues (AMNH 269823; V-882, −895, −896, −898, −912), Rivière Approuague (MNHN 1983.393). **Guyana**—*Cuyuni-Mazaruni,* Kartabo (AMNH 41910, 60641, 64130, 64132, 64133); *Potaro-Siparuni,* 5 km SE Surama (ROM 102970); "Essequibo River 13 mi from mouth" (BMNH 6.4.8.31 [holotype of *nitedulus*]; "R. Supinaam" (BMNH 10.9.29.18).

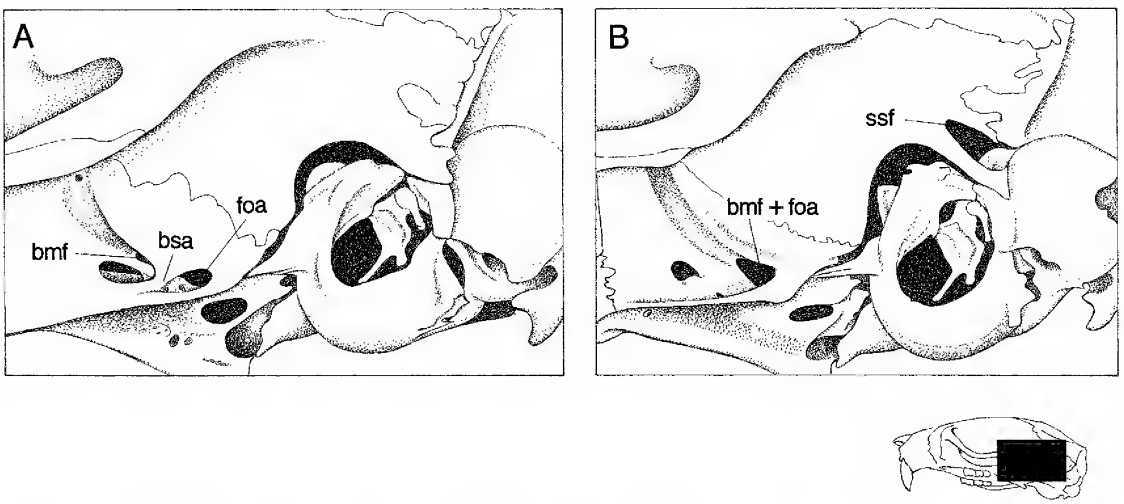

Fig. 57. Ventrolateral cranial views of *Oecomys auyantepui* (**A,** USNM 578015) and *O. paricola* (**B,** USNM 461389). In *O. auyantepui,* a bony strut of the alisphenoid (**bsa**) separates the buccinator-masticatory foramen (**bmf**) from the foramen ovale accessorius (**foa**), whereas in *O. paricola* the alisphenoid strut is absent and the two foramina are confluent (**bmf + foa**). Additionally, *O. auyantepui* consistently lacks the subsquamosal foramen (**ssf**), a prominent perforation in the posterolateral wall of the braincase that is consistently present in *O. paricola* and many other congeners.

TABLE 28

Measurements (mm) and Weights (g) of Adult *Oecomys auyantepui*[a]

	Type[b]	Guyana[c]	French Guiana[d]	Amapá (Brazil)[e]
Sex	male	6 males, 2 females, 2 unk.	10 males, 6 females	6 males, 4 females
HBL	126	115 (101–126) 7	112 ± 6 (100–121) 14	110 (90–125) 7
LT	133	120 (113–140) 6	126 ± 9 (112–144) 11	116 (100–140) 6
HF	25	24 (23–25) 9	24 ± 1 (24–26) 14	25 (24–27) 7
Ear	15[f]	16 (14–17) 8	16 ± 1 (15–18) 12	16 (14–17) 6
CIL	28.3	25.1 (23.0–27.0) 9	25.9 ± 1.1 (24.0–27.4) 16	25.3 (22.9–26.9) 8
LD	8.4	7.3 (6.4–8.0) 9	7.7 ± 0.4 (7.1–8.3) 15	7.4 (6.8–8.0) 9
LM	4.5	4.0 (4.0–4.1) 9	4.1 ± 0.1 (4.0–4.4) 15	4.1 (4.0–4.2) 9
BM1	1.3	1.2 (1.1–1.2) 9	1.2 ± 0.0 (1.2–1.2) 15	1.2 (1.1–1.2) 9
LIF	5.2	4.7 (4.0–5.2) 9	4.9 ± 0.2 (4.5–5.4) 16	4.6 (4.1–5.1) 8
BIF	2.3	2.2 (2.0–2.3) 9	2.3 ± 0.2 (1.9–2.6) 15	2.3 (1.9–2.6) 8
BPB	3.2	2.8 (2.5–3.0) 9	2.8 ± 0.3 (2.3–3.2) 14	2.9 (2.5–3.4) 9
BZP	2.6	2.2 (2.0–2.6) 9	2.3 ± 0.2 (2.1–2.6) 16	2.4 (2.0–2.7) 9
LIB	5.7	5.3 (4.9–5.8) 9	5.4 ± 0.2 (5.0–5.7) 15	5.3 (4.7–5.7) 9
ZB	16.3	14.9 (13.9–15.8) 9	15.1 ± 1.0 (13.6–16.6) 15	14.7 (13.0–15.7) 7
Wt	—	41 (32–51) 6	43 ± 10 (30–62) 11	41 (24–55) 8

[a] The sample mean, the observed range (in parentheses), and the sample size (N) are provided for each measurement with $N < 10$. The sample standard deviation is also provided for measurements with $N \geq 10$.

[b] AMNH 131156; from Auyantepui (1100 m elevation), Estado Bolívar, Venezuela.

[c] AMNH 64135, 269829, 269830; ROM 102944, 103051, 103052, 103244, 103288, 103433, 103502.

[d] Including Paracou vouchers: AMNH 266560, 266564, 267593, 267595, 267596; MNHN 1983.394, 1983.395, 1983.398, 1986.865, 1994.124, 1995.1027, 1995.1028, 1995.3235, 1998.1844; USNM 578015, 578019.

[e] USNM 393820, 393821, 394239–394243, 394246–394248.

[f] Measured from crown (Tate, 1939).

TABLE 29
Comparisons of State Frequencies for Two Qualitative Craniodental Characters in *Oecomys auyantepui* and *O. paricola*[a]

	auyantepui	*paricola*
Alisphenoid strut		
Bilaterally present	39	0
Unilaterally present	1	0
Bilaterally absent	1	20
Subsquamosal fenestra		
Bilaterally present	0	19
Bilaterally absent	41	0

[a] All examined specimens of *Oecomys auyantepui* are from the Guiana subregion of Amazonia, and all examined specimens of *O. paricola* are from south of the Amazon and east of the Tocantins. The museum catalog numbers of the specimens we examined are listed in the text. Because the tabulated frequency data are obviously highly improbable under the null hypothesis of no species difference for these characters, we omit formal test statistics.

external dimensions (table 30), there is sufficient morphometric overlap between them that no measurement is diagnostic. Most of the material at hand is preserved in fluid, so it is difficult to evaluate Anthony's statement that these species differ in fur color; however, no consistent differences were apparent in the few dried skins we examined. The species difference in tail length mentioned by Anthony (presumably meant to be considered in relation to the head-and-body) is also difficult to assess because we have not measured any specimens of *bicolor* ourselves (minor differences in measurement methodology can produce substantial artifactual divergence in computed ratios). Instead, two other characters are useful for field identification.

As observed by Anthony, the dorsal fur is longer in *Oecomys rutilus* than it is in *O. bicolor,* and the two species also differ in fur texture. In *rutilus,* the fur averages about 6–

Fig. 58. Tangled lianas in the understory of swampy primary forest at Paracou, capture site for *Oecomys auyantepui* (trapped 1.2 m above the ground, white arrow) and a typical substrate for other arboreal small mammals that occasionally descend to near ground level (e.g., *Micoureus demerarae* and *Oecomys rutilus*).

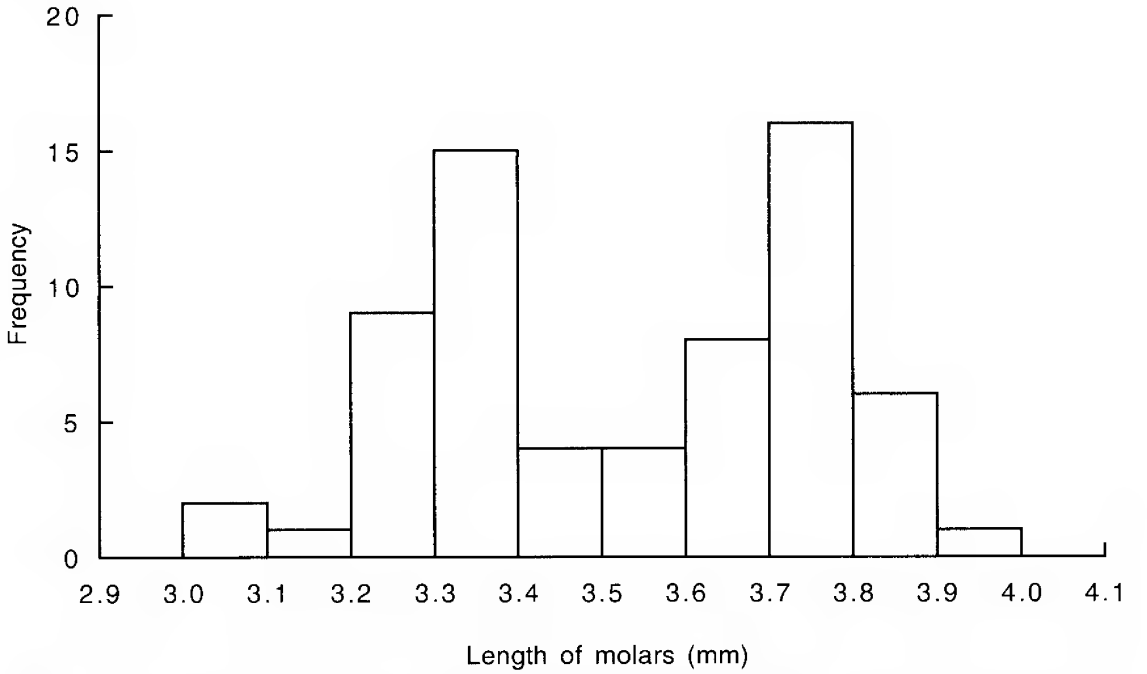

Fig. 59. Frequency histogram of upper molar toothrow length (LM) for 66 specimens of small *Oecomys* collected in the Guiana subregion of Amazonia. This sample includes material that we identify as *O. rutilus* (including Paracou vouchers and other conspecific specimens listed in the text) and *O. bicolor* (see text footnote 16).

8 mm middorsally near the rump, and it feels soft and lax when ruffled because the unresistant hairs return slowly to their normal (unruffled) condition. By contrast, the dorsal fur of *bicolor* is only 4–5 mm long in most specimens, and because *bicolor* is the larger species this absolute difference makes the pelage appear relatively much shorter. Also, the short fur of *bicolor* feels "crisp" to the touch because the stiffer hairs are more resistant to ruffling.

The tuft of hairs at the tail-tip is significantly longer in *Oecomys rutilus,* averaging 7.7 ± 1.4 mm (observed range: 5–11 mm, N = 19). In *O. bicolor,* this tuft measured 4–5 mm in all nine specimens we examined with intact tail tips. Since the long hairs of the tail tuft are often exposed to bending and compression in museum trays, it is probable that some of the tufts we measured were broken short, so the mean tuft length determined from fresh specimens with undamaged tails might be larger for both species than the values reported here. Nonethless, the difference is visually conspicuous and is useful for sorting skins in combination with other traits.

Skulls of *Oecomys bicolor* and *O. rutilus* differ in size (figs. 55, 56; table 30) and in the usual size-correlated proportions, but the incisive foramina are notably longer relative to the diastema in *bicolor* than in *rutilus,* a difference that is not attributable to standard patterns of muroid craniodental allometry. Although *bicolor* and *rutilus* are similar in most qualitative osteological traits, they differ significantly in the frequency of occurrence of the alisphenoid strut, an ossification that occurs bilaterally in most *rutilus,* but is bilaterally absent in most *bicolor* (table 31). Otherwise, these species are craniodentally similar, both having primitive carotid circulations (pattern 1 of Voss, 1988), beaded but unshelved supraorbital margins, and consistently large postglenoid foramina and subsquamosal fenestrae.

Although *Oecomys rutilus* and *O. bicolor* are widely distributed in the Guiana subregion of Amazonia, they have been collected

TABLE 30
Measurements (mm) and Weights (g) of Adult *Oecomys rutilus* and *O. bicolor*[a]

	Oecomys rutilus		
	Type[b]	French Guiana[c]	*Oecomys bicolor*[d]
Sex	female	14 males, 7 females, 1 unk.	4 males, 11 females
HBL	77	84 ± 6 (71–94) 21	94 ± 12 (76–118) 10
LT	94	98 ± 9 (80–111) 18	112 ± 7 (104–125) 9
HF	20	21 ± 1 (19–21) 21	22 ± 1 (21–23) 15
Ear	—	14 ± 1 (13–15) 19	13 ± 1 (12–14) 7
CIL	21.4	21.3 ± 1.0 (18.9–22.7) 21	23.9 ± 1.0 (22.7–25.9) 14
LD	6.2	6.0 ± 0.4 (5.2–6.4) 22	6.8 ± 0.4 (6.5–7.4) 14
LM	3.3	3.3 ± 0.1 (3.0–3.4) 22	3.8 ± 0.1 (3.6–3.9) 14
BMI	1.0	0.9 ± 0.0 (0.9–1.0) 22	1.1 ± 0.0 (1.0–1.1) 14
LIF	3.9	3.8 ± 0.2 (3.3–4.2) 22	4.6 ± 0.3 (4.1–5.2) 15
BIF	2.0	1.9 ± 0.2 (1.6–2.3) 21	2.1 ± 0.2 (1.9–2.5) 15
BPB	2.6	2.4 ± 0.2 (2.1–2.9) 21	2.7 ± 0.2 (2.4–3.1) 14
BZP	1.8	1.9 ± 0.2 (1.6–2.2) 21	2.2 ± 0.2 (2.0–2.4) 15
LIB	4.3	4.4 ± 0.2 (4.0–4.8) 21	4.8 ± 0.2 (4.5–5.1) 15
ZB	13.3	12.5 ± 0.8 (10.7–14.0) 21	13.8 ± 1.0 (12.5–15.5) 12
Wt	—	20 ± 5 (12–26) 17	28 ± 4 (23–34) 7

[a] Summary statistics for both species include the sample mean ± one standard deviation, the observed range (in parentheses), and the sample size.

[b] AMNH 42910, from Kartabo, Cuyuni-Mazaruni District, Guyana.

[c] Including Paracou vouchers: AMNH 266561, 267584, 267586, 267588–267591, 269121; MNHN 1983.400, 1995.1024–1995.1026, 1995.3236, 1995.3237, 1998.1845, 1998.1846; V-889, -892, -899, -900, -906, -913.

[d] AMNH 41910, 60641, 64130, 64132, 64133, 269823; BMNH 6.4.8.31, 10.9.29.18; MNHN 1983.393; ROM 102970; V-882, -895, -896, -898, -912. Note that all of these specimens are referrable to *Oecomys nitedulus*, a nominal species that Musser and Carleton (1993) synonymized with *O. bicolor*; typical *bicolor* (from eastern Ecuador) may have different measurements.

sympatrically only at Kartabo (Cuyuni-Mazaruni District, Guyana) and Les Nouragues (French Guiana). Musser and Carleton (1993) gave the range of *rutilus* as restricted to Guyana, Surinam, and French Guiana, but material from San Ignacio Yuruaní (Venezuela) and from 80 km N Manaus (Brazil) previously misidentified as *bicolor* (e.g., by Voss, 1991: table 23; Voss and Emmons, 1996: appendix 7) extend the range of this species east and south of the Guianas proper (fig. 60). Although we have not examined any material of *rutilus* from outside the Guiana subregion of Amazonia, the small unnamed *Oecomys* that Patton et al. (2000) reported from the Rio Juruá appears to be similar in some respects and merits close comparison in any future revisionary study.

The material we examined of *Oecomys rutilus* is remarkably uniform with little indication of significant variation among samples collected at widely separated localities. Thus, measurements of the Guyanese type (AMNH 42910), a mature adult female (not a subadult as conjectured by Hershkovitz, 1960), are all within the range of variation exhibited by French Guianan specimens (table 30). A few measurements of Brazilian and Venezuelan specimens exceed the observed range of variation for homologous measurements of French Guianan material, but the discrepancies are small in all cases.

OTHER SPECIMENS EXAMINED: **Brazil**—*Amazonas,* 80 km N Manaus (USNM 579992–579995). **French Guiana**—Cacao (MNHN 1983.400), Les Nouragues (AMNH 269822, V-889, −892, −899, −900, −906, −913), St.-Eugène (MNHN 1995.3236, 1995.3237, 1998.1845, 1998.1846). **Guyana**—*Cuyuni-Mazaruni,* Kartabo (AMNH 42910 [holotype], 142820); *Upper Demerara-Berbice,* Dubulay Ranch (AMNH 267745), 18 mi SW Kwakwani (AMNH 269828), Tropenbos (ROM 103482). **Surinam**—*Suriname,* Carolinakreek (FMNH

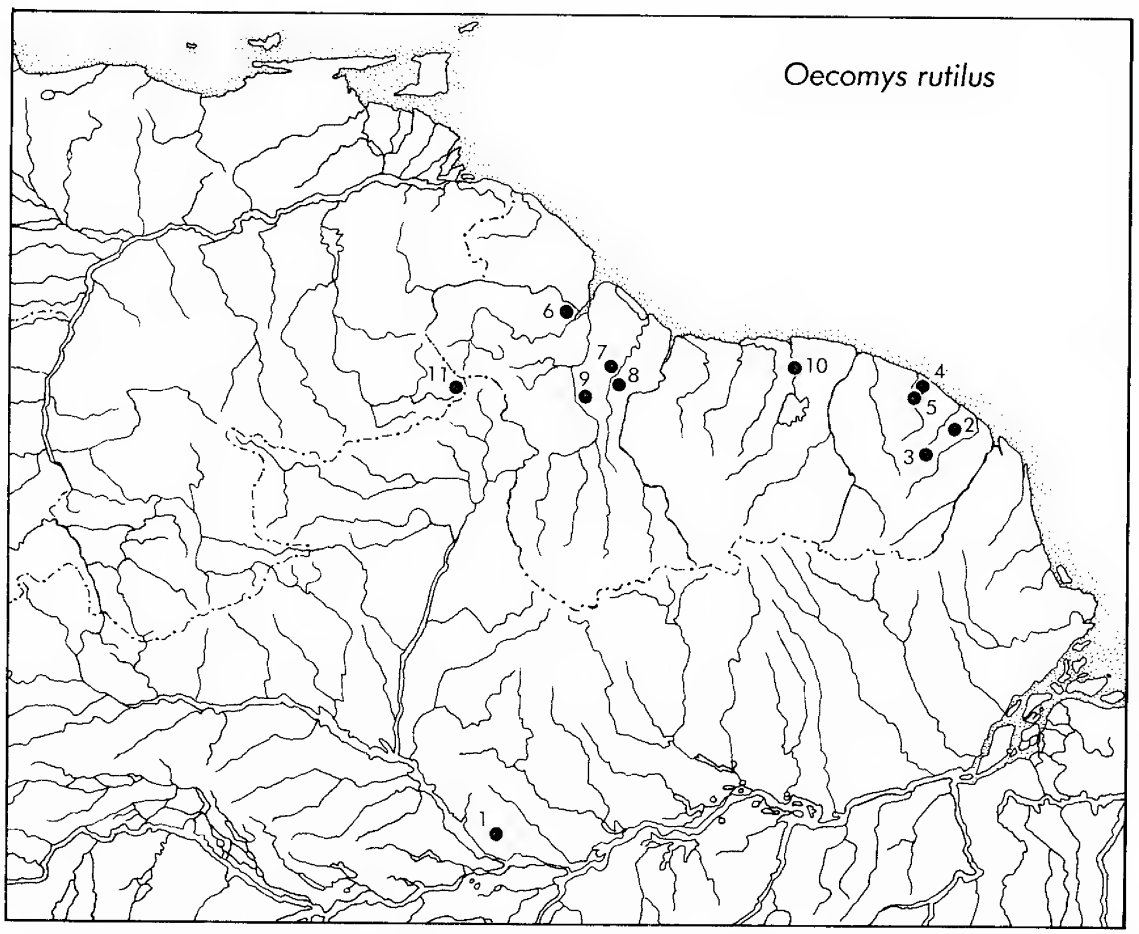

Fig. 60. Known collection localities for *Oecomys rutilus* based on specimens examined. **1,** BRAZIL, *Amazonas,* 80 km N Manaus; **2,** *French Guiana,* Cacao; **3,** FRENCH GUIANA, Les Nouragues; **4,** FRENCH GUIANA, Paracou; **5,** FRENCH GUIANA, St.-Eugène; **6,** GUYANA, *Cuyuni-Mazaruni,* Kartabo; **7,** GUYANA, *Upper Demerara-Berbice,* Dubulay Ranch; **8,** GUYANA, *Upper Demerara-Berbice,* 18 mi SW Kwakwani; **9,** GUYANA, *Upper Demerara-Berbice,* Tropenbos; **10,** SURINAM, *Suriname,* Carolinakreek; **11,** VENEZUELA, *Bolívar,* San Ignacio Yuruaní.

95591). **Venezuela**—*Bolívar,* San Ignacio Yuruaní (AMNH 257268, USNM 448576).

FIELD OBSERVATIONS: Although we saw small reddish mice racing along branches or lianas at night on many occasions, all of our definite records of *Oecomys rutilus* at Paracou are based on collected specimens. Of our 12 vouchers, 7 (58%) were taken in pitfall traps, 2 (17%) were shot at heights of 4–5 m in trees, 1 (8%) was taken in a Victor snap-trap tied to a liana 2 m above the ground, 1 was taken in a Sherman trap placed on a liana 30 cm above the ground, and 1 was taken in a platform trap 15.9 m above the ground. Six specimens (50%) were taken in well-drained primary forest, 4 (33%) in swampy primary forest, 1 (8%) in creekside primary forest, and 1 in roadside secondary growth. Both shot specimens were taken at night, and all of the other specimens were found in the traps at dawn.

Oligoryzomys fulvescens (Saussure)

VOUCHER MATERIAL: AMNH 267022, 267023; MNHN 1998.673. Total = 3 specimens.

IDENTIFICATION: Although the genus *Oli-*

TABLE 31
Comparison of Character-State Frequencies for Occurrence of the Alisphenoid Strut in *Oecomys bicolor* and *O. rutilus*[a]

	bicolor	*rutilus*	Totals
Bilaterally present	1	22	23
Unilaterally present	6	6	12
Bilaterally absent	28	4	32
Totals	35	32	67

$\chi^2 = 37.1$, df = 2, $p \ll 0.01$

$p = 3.8 \times 10^{-10}$ by Fisher's Exact Test

[a] Table entries are numbers of specimens. The chi-square value calculated from these data tests the null hypothesis of no species difference in proportions of specimens exhibiting alternative states for this character. Because of the small number of observations in several frequency classes, we also tabulate the exact probability calculated by Fisher's method.

goryzomys (formerly a subgenus of *Oryzomys*; see Carleton and Musser, 1989) has never been comprehensively revised, several publications have at least partially clarified the species-level systematics of *Oligoryzomys* in certain regions, notably Paraguay (Myers and Carleton, 1981), Bolivia (Olds and Anderson, 1987), and Central America (Carleton and Musser, 1995). Unfortunately, the *Oligoryzomys* of northern South America have received no revisionary attention to date. In a preliminary review of the genus, however, Carleton and Musser (1989) hypothesized that a single widespread polytypic species—*O. fulvescens*—extends from Mexico throughout most of Central America, thence southward into Colombia and northern Ecuador and eastward throughout Venezuela, Guyana, and Surinam. Included as subjective synonyms in a subsequent synopsis of *O. fulvescens* (see Carleton and Musser, 1995) were *costaricensis* J. A. Allen, *delicatus* J. A. Allen and Chapman, *navus* Bangs, *messorius* Thomas, *tenuipes* J. A. Allen, *munchiquensis* J. A. Allen, *lenis* Goldman, *mayensis* Goldman, *engraciae* Osgood, and *pacificus* Hooper. As defined geographically by Carleton and Musser (1989), *O. fulvescens* was not known to occur east of Surinam or south of the Amazon. Instead, populations of *Oligoryzomys* extending along the entire south bank of the Amazon from near the headwaters of that river to its mouth (near Belém) were identified as comprising a distinct species, *O. microtis* (J. A. Allen).

The taxonomic status of *Oligoryzomys* populations in French Guiana (first reported as *O. delicatus* by Charles-Dominique, 1993) and in the Brazilian state of Amapá (tentatively identified as *O. navus* by Carvalho, 1962) has yet to be critically evaluated. Because these regions constitute a geographic hiatus between the known ranges of *O. fulvescens* and *O. microtis* (as delimited by Carleton and Musser, 1989; see above), we compared our Paracou vouchers with typical material of both species.

Craniodental measurements of our three Paracou specimens (table 32) fall almost entirely within the range of morphometric variation observed by Carleton and Musser (1995) for a large sample of typical *Oligoryzomys fulvescens* (topotypes and other specimens from Veracruz, Mexico); the few exceptions are Paracou values (of BM1, BIF, BZP, and BB) that only exceed the observed range in homologous dimensions of typical *fulvescens* by 0.1 mm. Our vouchers are larger than average *fulvescens* from Mexico, but Carleton and Musser (1995) documented a southward cline of increasing size among their Central American samples; in craniodental measurements, our vouchers more closely resemble Costa Rican and Panamanian populations that Carleton and Musser referred to *O. f. costaricensis* than they do typical (Mexican) material.

The only noteworthy morphometric contrast between our Paracou vouchers and typical *Oligoryzomys fulvescens* appears to be the ratio of tail length to head-and-body length. That ratio is about 1.16 in our two specimens with intact tails, whereas the ratio of mean tail length to mean head-and-body length calculated from Carleton and Musser's (1995) data for Mexican *fulvescens* is 1.31. The same ratio for Costa Rican and Panamanian samples of *fulvescens* measured by those authors ranges from 1.27 to 1.44. In side-by-side comparisons, Mexican and Central American skins of *fulvescens* appear visibly longer-tailed than our Paracou vouchers.

Subtle qualitative cranial differences are present between our three specimens and the Mexican and Costa Rican exemplars of *fulvescens* with which we compared them. For

TABLE 32

Sex, Measurements (mm), and Weights (g) of *Oligoryzomys* Vouchers from Paracou with Comparative Data from Samples of Typical *O. fulvescens* and *O. microtis*

(All measurements from adult specimens.)

	Paracou vouchers				
	MNHN 1998.673	AMNH 267023	AMNH 267022	Typical *fulvescens*[a]	Typical *microtis*[b]
Sex	male	male	male	34 males, 23 females	10 males
HBL	78	81	85	—	89 (80–96) 9
LT	91	94	—	101 ± 7 (82–116) 55	91 (74–100)[c] 8
HF	22	22	21	21 ± 1 (20–24) 57	22 (20–23) 9
Ear	13	12	13	13 ± 1 (11–16) 55	—
CIL	19.6	19.7	20.3	—	20.5 (20.3–20.8) 4
LD	5.2	5.4	5.6	5.1 ± 0.4 (4.1–5.8) 50	5.8 (5.4–6.1) 7
LM	3.0	3.0	3.0	2.8 ± 0.1 (2.5–3.0) 50	3.2 (3.1–3.4) 6
BM1	0.9	0.9	1.0	0.9 ± 0.0 (0.8–0.9) 54	0.9 (0.9–1.0) 7
LIF	4.0	4.0	4.0	3.7 ± 0.4 (3.3–4.1) 50	3.9 (3.6–4.3) 10
BIF	1.9	1.6	1.9	1.6 ± 0.4 (1.4–1.8) 50	1.7 (1.5–1.8) 10
BPB	2.2	2.0	2.4	—	2.1 (1.9–2.3) 6
BZP	2.1	2.2	2.1	1.8 ± 0.1 (1.4–2.2) 50	2.1 (1.9–2.3) 10
LIB	3.5	3.4	3.5	3.4 ± 0.1 (3.1–3.7) 50	3.7 (3.3–3.9) 10
BB	10.0	10.1	10.6	10.0 ± 0.3 (9.4–10.5) 50	10.5 (10.3–10.7) 5
ZB	10.9	11.5	11.9	11.0 ± 0.4 (10.3–12.2) 50	12.2 (11.7–12.5) 4
LR	7.0	6.6	6.9	6.3 ± 0.4 (5.5–7.0) 50	7.1 (6.7–7.6) 7
Wt	14	16	19	—	—

[a] The mean ± one standard deviation, the observed range (in parentheses), and the sample size for measurements of topotypes and other specimens from Veracruz, Mexico (Carleton and Musser, 1995; unpublished data, Carleton in litt.). Rounding conventions account for all discrepancies between values tabulated here and those in Carleton and Musser's (1995) appendix.

[b] The mean, observed range (in parentheses), and sample size for measurements of Allen's (1916a) type series plus three topotypes: AMNH 37088–37097, 37157.

[c] Mean and range exclude an obviously bobbed-tail measurement of 20 mm recorded on the field label of one specimen (AMNH 37096).

example, the frontal sinuses appear slightly more inflated in the Mexican and Central American samples, producing a noticeably larger swelling behind the lacrimal bone in the front of the orbit than that seen in our French Guianan material. The rostrum also appears relatively longer and more slender, and the upper incisors perhaps less strongly opisthodont in Mexican and Central American specimens than in our vouchers. These are not conspicuous contrasts, however, and their possible taxonomic significance is difficult to assess without a careful study of the many hundreds of museum specimens that are now available from dozens of geographically intermediate localities. In other qualitative characters, including those that have previously been used to diagnose species of *Oligoryzomys* (e.g., the dorsal projection of the capsular process of the lower incisor alveolus, position of the incisive foramina relative to the toothrows, pelage color and texture), our vouchers appear to be indistinguishable from Mexican and Central American examples of *fulvescens*.

Confusingly, the Paracou material is also morphometrically similar to typical *Oligoryzomys microtis* as represented by Allen's (1916a) original series (and several topotypes, table 32) collected by Leo E. Miller on the "Lower Rio Solimoens (fifty miles above mouth)", a locality that can now be restricted with some confidence to a specific site on the *north* bank of the river.[17] Apparent

[17] According to Allen's (1916b) gazetteer of the Roosevelt Brazilian Expedition, Miller collected at this locality from 16 to 30 April 1914. A letter from Miller to F. M. Chapman (in the AMNH Ornithology archives) written in Manaus on 24 April 1914, however, states that he had just "... spent a week up on the Solimoens,

mensural differences between these very small samples (3 and 10 specimens, respectively) are unimpressive, especially when the considerable distance between collection localities (roughly 1300 km) is taken into account. Length of the molar toothrow is the only nonoverlapping measurement, but the mean sample difference (0.2 mm) is trivial. The few specimens at hand from immediately south of the Amazon (e.g., AMNH 95983, 188964) have toothrow measurements that do overlap those of our vouchers, so very large samples will probably be required to demonstate any significant divergence in this dimension between *Oligoryzomys* populations on opposite banks of the river, if any such difference in fact exists.

Allen's (1916a) original description of *Oligoryzomys microtis* emphasized the diagnostic value of pale coloration, relatively small ears, and short tail for distinguishing this species from other congeners. In coloration, however, Allen's material of *microtis* appears to be indistinguihable from typical *fulvescens* based on our side-by side comparisons of skins. Small differences in ear size are hard to evaluate without measurements taken in the flesh, which Leo E. Miller (the collector of Allen's specimens) did not record, and our visual comparisons of dried ears between typical material of *microtis* and *fulvescens* revealed no obvious size contrast. The reputedly diagnostic short tail of *microtis* is also hard to assess. Although Miller's field measurements of the type (AMNH 37091) indicate that its tail was slightly shorter than the head-and-body,[18] three paratypes (AMNH 37088, 37089, 37097) have an average ratio of tail to head-and-body of 1.20. Because Miller did not indicate whether his measurements were of complete or bobbed tails (AMNH 37096 has an obviously bobbed-tail measurement of 20 mm with no accompanying notation to that effect), and because most of his skins no longer have intact tailtips (the result of bending and compression in museum trays), it is now impossible to evaluate the ratio of tail to head-and-body length in Allen's series. Other specimens of *microtis* (sensu Carleton and Musser, 1989), however, are not very short-tailed: one specimen from the south bank of the lower Amazon (AMNH 203400) has a tail:body ratio of 1.17, whereas another (AMNH 188964) has an improbably large ratio of 1.57. Given the usual methodological inaccuracies associated with muroid tail measurements (Howell, 1924), any taxonomic inferences based on this dimension in the small samples at hand would be premature.

We found no obvious qualitative characters to distinguish *Oligoryzomys fulvescens* (as represented by our Mexican and Central American exemplars) from typical *O. microtis,* and in view of the negligible morphometric differences indicated by table 32 we are unable to confidently assign our Paracou material to one or the other taxon. Although

with a [G]erman friend, and got some nice things in the mammal line . . . but I hope to go to another fazenda within a day or two." Miller therefore visited (or intended to visit) two localities near Manaus between 16 and 30 April. Perplexingly, Miller's skin tags give only "Solimoens" as the locality where he worked in this interval, and his field catalog (AMNH Mammalogy archives) contains no additional geographic information. Fortunately, this problem did not escape the notice of mammalogists who were still in time to obtain at least a partial first-hand clarification: in a letter dated 4 June 1945, G. H. H. Tate wrote Miller (then retired and living in Connecticut) asking him to provide additional geographic details about the types of *Proechimys kermiti* (collected 20 April 1914) and *Oligoryzomys microtis* (collected 29 April 1914). Miller replied in a letter dated 6 June 1945 that "After a short time in Manaos, I went down the Rio Negro and up the Solimoes about 50 or 60 miles to make the collections on the *North* bank of the river. The location is approximately between 3° and 4° S Lat., and Long. 61°. I think this will locate the spot closely enough for your purposes." (italics ours; correspondence in AMNH Mammalogy archives). Because Miller did not mention collecting at separate localities on the 20th and the 29th, the second sojourn from Manaus mentioned in his letter to Chapman of 24 April 1914 may have been a return trip to his previously productive site. Based on Miller's reply to Tate, Moojen (1948) published the restricted type locality of *P. kermiti* as Manacaparú, a settlement located 70 km WSW of Manaus on the north bank of the lower Solimões at 3°08′S, 60°01′W (Paynter and Traylor, 1991). We assume that the type of *O. microtis* was collected at the same place.

[18] Miller's original measurements, recorded in pencil on a small field label tied to the right hindfoot of the type skin, were correctly reported by Allen (1916a) as 183 mm (total length), 90 mm (tail), and 20 mm (hindfoot). However, Olds and Anderson (1987: 271) stated that ". . . the tail of the holotype is more than half the total length, a discrepancy noted by Goodwin (1953)." In fact, Goodwin (p. 299) did not note any discrepancy and reported the same external measurements as Allen.

an obvious implication of the preceding discussion is that *fulvescens* and *microtis* are conspecific, it is also possible that multivariate analyses of larger samples could detect morphological discontinuities that are not now apparent; karyological and biochemical comparisons among key geographic populations could likewise contribute to an assessment of these and other phenotypically similar nominal taxa of *Oligoryzomys* as valid species. Lacking the time to undertake such a critical revisionary study for this faunal report, we simply apply the older name to our Paracou material.

OTHER SPECIMENS EXAMINED: **Brazil**—*Amazonas,* near Manacaparú on north bank of lower Rio Solimões (AMNH 37088, 37089, 37091 [holotype of *microtis*], 37092–37097, 37157); *Pará,* Capim (AMNH 188964, 203400), Pôrto de Moz (AMNH 95983), Vilarinho do Monte (AMNH 95984–95986, 95997). **Costa Rica**—*Puntarenas,* Cañas Gordas (AMNH 142440–142458, 142490–142495, 142500). **Mexico**—*Veracruz,* Jalapa (AMNH 12536/10846–12541/10851, 12543/10853–12549/10959, 12583–12585).

FIELD OBSERVATIONS: All of our definite records of *Oligoryzomys fulvescens* at Paracou are based on collected specimens. All three of our vouchers were caught by hand at night in roadside secondary growth (fig. 13), where two were encountered running on the ground through sparse weeds and the third was climbing among the dried leaves of a felled tree.

Oryzomys Baird

The Amazonian species of *Oryzomys* were recently revised by Musser et al. (1998), whose species-level taxonomy is followed herein. As a group, Amazonian species of *Oryzomys* are easily distinguished from other sympatric rodents by external characters. These are medium-sized murids, ranging in average adult body weight from about 40 to 80 g. The dorsal fur is soft (not spiny) and varies in color (depending on species, age, and stage of molt) from rich reddish or tawny hues to drab brown. The ventral fur is superficially whitish or whitish gray, contrasting abruptly in color with the dorsal fur (except in juveniles), but the ventral hair bases are always dark gray. The mystacial vibrissae are short, not extending beyond the tips of the pinnae when laid back alongside the head. The dorsal surface of the hindfoot is unmarked by dark metatarsal spots or bands, and the naked plantar surface is pigmented (grayish in life and in fluid-preserved material, blackish on dried skins). The hindfoot (fig. 53A) appears narrow because the three central pedal digits (II, III, and IV) are much longer than the outer digits (I and V); the fifth digit is not semi-opposable (its claw not extending to the end of the first phalange of dIV). Tails are usually at least partially bicolored (at least near the base), average about as long as (never much shorter or longer than) the combined length of head-and-body, and appear quite naked (a sparse caudal pelage is visible only under magnification). Contrasting external characters of *Oecomys* species, which are sometimes misidentified as *Oryzomys* (and vice versa) by fieldworkers, are given in the introductory account for that genus (above).

Three species, *Oryzomys macconnelli, O. megacephalus,* and *O. yunganus,* occur sympatrically at Paracou as they probably do throughout the Guiana subregion of Amazonia (see range maps in Musser et al., 1998). Whereas adult specimens of *O. macconnelli* are easily recognized by external characters, accurate field identifications of *O. megacephalus* and *O. yunganus* are more difficult. Juvenile *Oryzomys,* which lack the diagnostic external dimensions and coloration of adults, cannot be reliably identified in the field.

Oryzomys macconnelli Thomas

VOUCHER MATERIAL: MNHN 1998.674–1998.676. Total = 3 specimens.

IDENTIFICATION: Our three Paracou vouchers (collected by O. Henry, see below), together with additional material that we examined from other French Guianan localities, agree with Musser et al.'s (1998: 225–232) description of *Oryzomys macconnelli,* an identification that we confirmed by direct comparison with Thomas's (1910) type series from the Supenaam River, Guyana. Although the French Guianan material averages small-

er than the type series in many dimensions (table 33), most French Guianan specimens are young adults (with lightly worn molars) whereas the type series is composed of older specimens (with more advanced toothwear). In the absence of other noteworthy differences between the two series, most of the observed measurement divergence could be attributed to sample age composition. The longer molar rows of the Guyanese series, however, cannot be attributed to advanced age, and the observation of even longer toothrows in some Venezuelan series (LM averages 5.2 mm in 12 specimens that we measured from Estado Bolívar) suggests that a real east-to-west size gradient may exist among *O. macconnelli* populations from the Guiana subregion of Amazonia. Western Amazonian samples are even more divergent morphometrically (Musser et al., 1998: fig. 106), and available karyotypes from western Amazonia differ dramatically from those of the single population sampled for chromosomes in the Guianan subregion (op. cit.: fig. 105). In the event that western Amazonian populations currently referred to *O. macconnelli* merit formal taxonomic recognition, the name *O. mureliae* J. A. Allen, based on a specimen collected in eastern Colombia, is available (Musser et al., 1998: 278–280). The Paracou population, however, is unambiguously assignable to *O. macconnelli,* or to the nominate race if a trinomial nomenclature is adopted.

Based on the samples at hand from Paracou and other localities in French Guiana, adult specimens of *Oryzomys macconnelli* can be readily distinguished in the field from *O. megacephalus* and *O. yunganus* by their larger external dimensions (especially hindfoot length: tables 33, 34), brighter pelage colors (redder dorsally and whiter ventrally versus drab brown dorsally and grayer ventrally in *megacephalus* and *yunganus*), longer dorsal fur (12–15 mm versus <10 mm in *megacephalus* and *yunganus*), sharply bicolored tails that are slightly longer than heads-and-bodies (versus indistinctly bicolored or unicolored-dark and shorter in *megacephalus* and *yunganus*), and six plantar pads on the hindfoot (versus five in most *yunganus,* see below). *Oryzomys macconnelli* also has a longer rostrum than either of the other species with which it is sympatric in French Guiana, a contrast that is obvious in cranial comparisons (Musser et al., 1998) but can also be seen in living specimens.

OTHER SPECIMENS EXAMINED: **French Guiana**—Arataye (MNHN 1983.371–1983.373, 1986.276), St.-Eugène (MNHN 1994.126, 1994.127, 1995.208, 1998.1842–1998.1844), Saül (MNHN 1983.365, 1983.367). **Guyana**—"River Supinaam" (BMNH 10.5.4.29–10.5.4.34 [type series]). **Venezuela**—*Bolívar,* San Ignacio Yuruaní (AMNH 257236–257238; MHNLS 7831, 7836, 7880, 8075, 8076, 8088; USNM 448584–448586).

FIELD OBSERVATIONS: Our only records of *Oryzomys macconnelli* at Paracou are based on three specimens trapped by O. Henry, none of which were accompanied by ecological information.

Oryzomys megacephalus Fischer

Figure 53A

VOUCHER MATERIAL: AMNH 266494, 266497, 266498, 266501, 266502, 266504, 266508, 266514, 266515, 266518, 266521, 266523, 266525, 266527–266530, 266533, 266535, 266538, 266539, 266541, 267018, 267566; MNHN 1995.999–1995.1010. Total = 36 specimens.

IDENTIFICATION: At Paracou, and apparently throughout most of Amazonia, *Oryzomys megacephalus* (formerly *O. capito,* see below) occurs sympatrically with another morphologically similar species, *O. yunganus* (see range maps in Musser et al., 1998). Both are drab-colored *Oryzomys* with brownish dorsal fur, whitish-gray ventral fur, and indistinctly bicolored or unicolored-dark tails that average a little shorter than heads-and-bodies. Comparisons of external measurements from our voucher material suggest that French Guianan *O. megacephalus* have slightly longer tails than sympatric *O. yunganus,* but the difference in average values for the ratio LT/HBL is small (0.94 versus 0.89) and insufficient for field identification because of overlapping variation (the observed range in this ratio among our vouchers is 0.78–1.03 for *megacephalus,* 0.69–1.13 for *yunganus*). Our measurement data suggest no appreciable species difference in absolute or relative size of the hindfoot. On

TABLE 33
Measurements (mm) and Weights (g) of *Oryzomys macconnelli* from French Guiana and the Type Locality[a]

	French Guiana[b]	Supenaam River, Guyana[c]
Sex	8 males, 3 females, 3 unk.	1 male, 2 females, 3 unk.
HBL	139 (128–148) 6	—
LT	144 (135–162) 8	—
HF	34 ± 1 (32–36) 13	35 (33–36) 6
Ear	22 (20–24) 6	22 (21–24) 5
CIL	29.0 ± 1.4 (26.0–30.9) 14	30.6 (29.5–31.9) 4
LD	8.7 ± 0.6 (7.4–9.4) 14	9.4 (8.9–10.1) 5
LM	4.8 ± 0.2 (4.5–5.1) 14	5.0 (4.8–5.2) 4
BM1	1.4 ± 0.1 (1.3–1.5) 14	1.4 (1.4–1.5) 5
LIF	5.0 ± 0.4 (4.3–5.5) 14	5.4 (5.0–5.9) 5
BIF	2.6 ± 0.2 (2.2–3.0) 14	2.9 (2.8–3.0) 5
BPB	3.3 ± 0.3 (2.6–3.7) 14	3.5 (3.4–3.7) 3
BZP	3.3 ± 0.2 (3.0–3.6) 13	3.6 (3.4–3.8) 5
LIB	5.4 ± 0.2 (4.9–5.8) 14	5.7 (5.5–5.8) 5
ZB	15.6 ± 1.2 (13.4–16.9) 12	16.5 (16.1–16.9) 4
Wt	75 (58–80) 8	—

[a] Sample statistics include the mean ± one standard deviation (for N ⩾ 10), the observed range (in parentheses), and the sample size.

[b] Including Paracou vouchers: MNHN 1983.367, 1983.371–1983.373, 1986.276, 1994.126, 1994.127, 1995.208, 1998.674–1998.676, 1998.1842–1998.1844.

[c] The type series: BMNH 10.5.4.29–10.5.4.34.

average, *megacephalus* has somewhat brighter adult dorsal pelage than *yunganus,* but the difference is subtle and not useful for field identification.

The only external character potentially useful for distinguishing *Oryzomys megacephalus* from *O. yunganus* in the field is the number of plantar pads on the hindfoot (for illustrations, see Musser et al., 1998: fig. 17). Almost all specimens of *megacephalus* have six plantar pads: thenar, hypothenar, and four interdigitals. By contrast, most French Guianan *yunganus* have five pads because the hypothenar is absent (table 35). One Paracou specimen of *megacephalus* (AMNH 266527), however, lacks the hypothenar completely on one foot and has only an indistinct hypothenar on the other. Similarly, a few *yunganus* from Paracou (e.g., AMNH 266495, MNHN 1995.994) have distinct hypothenars on one or both hindfeet. Based on our tabulation of trait frequencies, a conservative approach to identifying these species in the field in French Guiana (classifying animals with six distinct plantar pads on both hindfeet as *megacephalus* and those with only five pads on both feet as *yunganus*) would leave an estimated 3% of specimens undetermined (i.e., those with asymmetrical numbers of pads, plus those with indistinct hypothenars on both feet) and would result in an expected error rate of about 5% (mostly *yunganus* misidentified as *megacephalus*).

The only truly reliable basis for identifying *megacephalus* and *yunganus* is cleaned cranial material, from which diagnostic molar characters can be determined. All of the Paracou vouchers we identify as *megacephalus* have (1) the long paraflexus and single fossette on M2, and (2) the long hypoflexid, diagonal median murid, and lack of fossetid on m2 described and illustrated by Musser et al. (1998). By contrast, specimens we identify as *yunganus* have (1) a short paraflexus and two fossettes on M2, and (2) a short hypoflexid separated from a lingual fossetid by a less oblique median murid on m2 (op. cit.). Our multivariate statistical analyses of cranial measurement data from Paracou vouchers identified by these molar traits reveal that specimens of *megacephalus* have, on average, wider incisive foramina and narrower zygomatic plates than like-sized examples of *yunganus.* However, measurement variation is too extensive for cranial proportions to be used as the sole basis for species identification at this locality. Although molar measurements differ significantly between sympatric samples of *megacephalus* and *yunganus* from some parts of Amazonia (Musser et al., 1998: table 8), these species do not diverge in dental dimensions at Paracou.

Husson (1978) and most other recent authors have called this species *Oryzomys capito* (Olfers), but Tate (1939) referred Guianan populations to *O. laticeps* (Lund). Both *capito* Olfers and *megacephalus* Fischer are based on Azara's (1801) description of the "Rat Seconde ou Rat à Grosse Tête" from Paraguay. Musser et al. (1998) designated a Paraguayan neotype for *megacephalus* and explained why this name should replace *capito* (a junior objective synonym). Musser and his colleagues also diagnosed *Oryzomys la-*

TABLE 34
Measurements (mm) and Weights (g) of *Oryzomys megacephalus* and *O. yunganus* from Paracou[a]

	megacephalus[b]	*yunganus*[c]
Sex	10 males, 17 females, 1 unk.	5 males, 6 females
HBL	119 ± 9 (99–139) 28	115 ± 14 (84–131) 11
LT	111 ± 8 (100–130) 28	102 ± 9 (90–120) 9
HF	28 ± 1 (26–31) 28	28 ± 1 (25–29) 11
Ear	19 ± 1 (17–21) 28	18 ± 1 (17–20) 11
CIL	26.7 ± 1.5 (23.0–29.2) 28	26.0 ± 1.3 (23.8–27.7) 11
LD	7.8 ± 0.5 (6.4–8.6) 28	7.8 ± 0.6 (6.8–8.6) 11
LM	4.5 ± 0.2 (4.2–5.0) 28	4.4 ± 0.1 (4.3–4.6) 11
BM1	1.3 ± 0.0 (1.2–1.4) 28	1.3 ± 0.0 (1.3–1.4) 11
LIF	4.3 ± 0.4 (3.4–4.9) 28	4.3 ± 0.3 (3.9–4.8) 11
BIF	2.3 ± 0.2 (1.9–2.6) 28	1.9 ± 0.2 (1.7–2.2) 11
BPB	2.8 ± 0.3 (2.4–3.4) 28	2.9 ± 0.3 (2.4–3.4) 11
BZP	3.0 ± 0.3 (2.2–3.5) 28	3.2 ± 0.3 (2.9–3.7) 11
LIB	5.1 ± 0.2 (4.6–5.4) 28	5.0 ± 0.2 (4.8–5.3) 11
ZB	14.4 ± 0.9 (12.3–16.4) 28	14.1 ± 0.7 (13.0–14.9) 11
Wt	42 ± 9 (24–56) 27	39 ± 8 (26–53) 11

[a] Summary statistics include the mean ± one standard deviation, the observed range (in parentheses), and the sample size.

[b] AMNH 266494, 266497, 266498, 266501, 266502, 266504, 266508, 266514, 266515, 266518, 266521, 266523, 266527, 266528, 266530, 266533, 266535, 266538, 266539, 266541, 267018, 267566; MNHN 1995.1000, 1995.1001, 1995.1003, 1995.1007, 1995.1008, 1995.1010.

[c] AMNH 266495, 266496, 266503, 266516, 266517, 266520, 267017, 267567; MNHN 1995.993, 1995.997, 1995.998.

ticeps as a distinct species restricted to the Atlantic rainforest region of southeastern Brazil.

As understood by Musser et al. (1998), *Oryzomys megacephalus* occurs throughout Amazonia and extends southward into the Paraná basin of eastern Paraguay. Morphometric, karyotypic, and molecular data summarized by Musser and his colleagues, however, strongly suggest that western Amazonian populations (characterized by large size, diploid counts of 52 chromosomes, and distinctive mtDNA haplotypes) are genetically and evolutionarily distinct from Paraguayan and eastern Amazonian populations (characterized by small body size, diploid counts of 54 chromosomes, and different mtDNA sequences). Although Musser et al. (1998) recognized this dichotomy, they emphasized the difficulty of identifying geographically intermediate samples as belonging to either the eastern or western clades by morphological criteria and provisionally regarded all of their *megacephalus*-like Amazonian material as conspecific. Patton et al. (2000) subsequently recognized the western Amazonian form as a distinct species, *O. perenensis* J. A. Allen, a decision with which we concur.

In fact, *Oryzomys megacephalus* may be composite even in the restricted sense of Patton et al. (2000) because their cytochrome-b

TABLE 35
Frequency of Occurrence of the Hypothenar Pad on the Hindfeet of *Oryzomys megacephalus* and *O. yunganus* from French Guiana[a]

		Present[b]		
	N	On both feet	On one foot	Absent
megacephalus	87	86(lg)	1(vs)	0
yunganus	28	6(lg) + 2(vs)	0	20

[a] Paracou vouchers plus specimens examined from other localities in French Guiana (see text accounts for museum numbers). Not all specimens examined could be scored for occurrence of the hypothenar pad.

[b] Feet with the hypothenar present have a total of six plantar pads; feet without a hypothenar have five pads. Well-developed hypothenar pads are indicated as "large" (lg); indistinct hypothenars, always much reduced in size and usually lacking a distinct outline, are indicated as "very small" (vs).

sequence analyses (op. cit.: fig. 97) suggest that samples of the small 2N = 54 taxon from north and south of the Amazon form reciprocally monophyletic groups. In the event that these geographic moieties should prove to be diagnosably different by additional criteria, the oldest available name for the northern form (to which our Paracou sample is presumably referable) is *velutinus* J. A. Allen and Chapman (1893), based on a holotype collected at Princestown, Trinidad.

OTHER SPECIMENS EXAMINED: **French Guiana**—Arataye (MNHN 1986.287–1986.293, 1986.295, 1986.296, 1986.298–1986.301, 1986.314, 1986.878–1986.880, 1986.882), Cacao (MNHN 1980.275, 1983.370, 1986.278, 1986.279, 1986.316, 1986.493–1986.499, 1986.501, 1986.506, 1986.511, 1986.514, 1986.531, 1986.533), Camopi (MNHN 1982.600, 1982.620), Cayenne (MNHN 1970.225, 1986.317, 1986.319, 1986.952, 1986.953), "Marais de Kaw" (MNHN 1986.1106, 1986.1107), Rorota (MNHN 1986.954, 1986.955), Piste St.-Élie km 16 (MNHN 1986.884–1986.886), Saül (MNHN 1981.181, 1983.368, 1983.369, 1986.489, 1986.492, 1986.518, 1986.521, 1986.525), Sauts de l'Itany (MNHN 1962.1024–1962.1028), Trois Sauts (MNHN 1981.150, 1982.616–1982.619, 1982.623–1982.627, 1986.283, 1990.908–1990.910).

FIELD OBSERVATIONS: All of our definite records of *Oryzomys megacephalus* at Paracou are based on collected specimens. Of our 36 vouchers, 23 (64%) were taken in Sherman or Victor traps set on the ground, 7 (19%) were taken in Sherman or Victor traps tied to lianas 0.3–1.2 m above the ground, 5 (14%) were shot on the ground, and 1 (3%) was taken in a pitfall. Microhabitat notes accompanying 26 specimens shot or trapped on the ground record 18 captures under or beside logs, 4 captures under the roots or buttresses of fallen trees, 2 captures under tangled branches of fallen trees, 1 capture at the base of a buttressed tree, and 1 capture at the entrance to a hollow log. All of the shot specimens were encountered at night, and all of the other specimens were found in traps at or near dawn. Twenty-two specimens (61%) were taken in well-drained primary forest, 3 (8%) in swampy primary forest, 2 (6%) in creekside primary forest, 5 (14%) in primary forest of unspecified character, and 4 (11%) in secondary vegetation. See table 36 and the following account for capture-habitat comparisons with *O. yunganus.*

TABLE 36
Comparison of Capture-Habitat Frequencies between *Oryzomys megacephalus* and *O. yunganus* Trapped in Primary Forest at Paracou[a]

	Capture habitat		
	Well-drained forest	Swampy or creekside forest	Totals
megacephalus	22	5	27
yunganus	7	8	15
Totals	29	13	42
$\chi^2 = 5.5$, df = 1, $p < 0.05$			

[a] Table entries are numbers of captures. The chi-square value calculated from these data tests the null hypothesis of no interspecific difference in proportions of captures by habitat.

Oryzomys yunganus Thomas

VOUCHER MATERIAL: AMNH 266495, 266496, 266503, 266510, 266511, 266513, 266516, 266517, 266520, 266532, 267017, 267567; MNHN 1995.993–1995.998. Total = 18 specimens.

IDENTIFICATION: See the account above for morphological comparisons with *Oryzomys megacephalus,* the only species with which *O. yunganus* could plausibly be confused.

Long unrecognized as a member of the Guianan fauna, *O. yunganus* was recently revised by Musser et al. (1998), who documented the extensive Amazonian distribution of this species by mapping all known collection localities (op. cit.: fig. 14). As noted by Musser and his colleagues, the geographic samples they refered to *O. yunganus* exhibit considerable divergence in body size. Especially notable are specimens from Guyana, Surinam, French Guiana, and eastern Amazonian Brazil, which are diminutive by comparison with specimens from Venezuela, Colombia, Ecuador, Peru, and western Brazil. For example, the observed range of variation in crown length of the upper molar series (LM) among our vouchers (4.3–4.6 mm; table 34) does not overlap with the observed

range of variation among 52 specimens (including the type) that we measured from Colombia, Ecuador, Peru, and Bolivia (4.8–5.6 mm). Additionally, French Guianan samples of *O. yunganus* differ conspicuously from western Amazonian samples in the frequency of occurrence of the hypothenar pad on the hindfoot (Musser et al., 1998: table 7). The currently accepted provisional hypothesis, that these and other differences among samples currently referred to *O. yunganus* represent intraspecific geographic variation, merits testing by additional collecting at intermediate localities (op. cit.: p. 109), and by analyzing molecular sequence data from Guianan and western Amazonian populations (as by Patton et al., 2000).

OTHER SPECIMENS EXAMINED: **Bolivia**—*Cochabamba,* Charuplaya (BMNH 2.1.1.39 [holotype]). **Colombia**—*Caquetá,* Tres Troncos (FMNH 72036, 72051, 72066); *Meta,* La Macarena (FMNH 58778, 58779, 87969, 87970); *Putumayo,* Río Mecaya (FMNH 72067). **Ecuador**—*Pastaza,* Río Capahuari (FMNH 43268, 43271), Río Yana Rumi (FMNH 43265). **French Guiana**—Arataye (MNHN 1986.294, 1986.297, 1986.313, 1986.881, 1986.883), Cacao (MNHN 1986.490), Cayenne and Rorota (MNHN 1986.322, 1986.324, 1986.326, 1986.327, 1986.800–1986.803), Kaw (MNHN 1986.1105). **Peru**—*Cuzco,* Hacienda Cadena (FMNH 65704, 66399, 66401, 68630, 68631), Quincemil (FMNH 75242, 75253, 75254, 75257, 75259, 75261–75264, 75272; *Huánuco,* Chinchao (FMNH 23721, 23722), Hacienda Buena Vista (FMNH 24544, 24547, 24548); *Loreto,* Río Pastaza (BMNH 54.421, 54.422, 54.425, 54.429, 54.430); *San Martín,* Moyobamba (FMNH 19376, 19387, 19392), Puca Tambo (BMNH 26.5.3.31–26.5.3.38, 26.5.3.40–26.5.3.42; FMNH 19787); **Surinam**—*Nickerie,* Kayserberg Airstrip (FMNH 93284, 93286).

FIELD OBSERVATIONS: All of our definite records of *Oryzomys yunganus* at Paracou are based on collected specimens. Our 18 vouchers represent only 16 sampling events, however, because pairs of juvenile individuals were taken in the same trap on two occasions. Of these 16 independent captures, 15 (94%) were in Sherman traps set on the ground, and one was in a pitfall. All of our specimens were found in the traps at or near dawn. Seven captures (44%) were in well-drained primary forest, another 7 were in swampy primary forest, 1 (6%) was in creekside primary forest, and 1 was in primary forest of unspecified character. Microhabitat notes accompanying 15 specimens record 4 captures under or beside logs, 3 captures at the bases of trees, 3 captures in dense undergrowth unsheltered by woody objects, 2 captures under tangled dead branches, 2 captures under fallen palm fronds, and 1 capture among the stilt roots of a standing tree.

Our capture data from Paracou are broadly consistent with specimen counts from other Amazonian localities (summarized by Musser et al., 1998) in suggesting that *Oryzomys yunganus* is less abundant than *O. megacephalus* wherever these species occur sympatrically. Although we sometimes caught both species in the same trapline on the same date, statistical comparisons of capture frequencies by habitat (table 36) suggest that *O. yunganus* prefers moister primary forest habitats (swamp or creekside formations) than does *O. megacephalus.* The latter species was also trapped above ground level on lianas, and in secondary vegetation, situations in which *O. yunganus* was not encountered. Future ecological studies of Amazonian rodent communities should test the hypothesis that *O. yunganus* is a habitat specialist by comparison with *O. megacephalus,* but we caution that destructive sampling (or molecular typing, as by Lavergne et al., 1997; Steiner et al., 2000) will be necessary in order to obtain reliable taxonomic identifications for this purpose.

Rhipidomys nitela Thomas

Figure 53C, 61B, 62A

VOUCHER MATERIAL: AMNH 267021, 267580, 267582, 267583, 267594; MNHN 1995.1011, 1995.1012. Total = 7 specimens.

IDENTIFICATION: The ten nominal taxa of *Rhipidomys* based on type material collected in the Guiana subregion of Amazonia appear to represent four valid species that can be readily distinguished by external and craniodental characters. *Rhipidomys macconnelli* de Winton (1900) (including *subnubis* Tate, 1939) and *R. wetzeli* Gardner (1989) have

TABLE 37
Diagnostic Characters and Geographic Ranges of *Rhipidomys mastacalis, R. nitela,* and *R. venezuelae*[a]

	mastacalis[b]	*nitela*[c]	*venezuelae*[d]
Length of molars[e]	5.0 (4.9–5.3) 6	4.4 (4.1–4.8) 62	5.2 (4.9–5.6) 50
Tail tuft	long and prominent	long and prominent	absent or inconspicuous
Karyotype	2N = 44[f]	2N = 48[g]	unknown
Distribution	Mata Atlantica of southeastern Brazil	Guiana and Southeastern subregions of Amazonia	moist and dry forests of northern Venezuela and northeastern Colombia

[a] Based on Tribe (1996) and other published and unpublished sources identified below.

[b] Specimens that we examined and measured are from the type locality (Lagoa Santa, Minas Gerais state, Brazil). Housed in the Universitets Zoologiske Museum, Copenhagen, these consist of Lund's (1840) original series (L16–L19) and topotypes subsequently collected by J. Reinhardt and E. Warming (CMUZ 292, 293, 398). The type of Lund's *Mus mastacalis* (original number L16, subsequently cataloged as CMUZ 291) is identified by the notation "Lund's 1ste Expl." in H. Winge's handwriting.

[c] See text for specimens examined.

[d] The specimens we examined are all from Venezuela: *Aragua,* Camp Rangel (USNM 314182), Rancho Grande (USNM 517589); *Falcón,* Cerro Socopo (USNM 442133); *Lara,* Río Tucuyo (AMNH 131027, 131029–131031, 131037, 131039–131042, 131046, 131049, 131050, 131055, 131058–131061, 131063, 131066, 131067, 131069, 131071, 131074, 131076–131079, 131081–131084); *Mérida,* Jají (FMNH 21827), near Mérida (BMNH 96.11.1.1 [type], 99.12.1.4, 99.12.1.5, 99.12.1.8–99.12.1.10, 5.2.5.13, 8.6.24.4; FMNH 18887, 29443), Río Chama (FMNH 21826); *Trujillo,* 10 km NW Valera (USNM 371251); *Zulia,* Misión Tukuko (MHNLS 7746, 7792; USNM 448630).

[e] Mean, observed range (in parentheses), and sample size based on specimens examined and measured by us.

[f] Karyotypes of *Rhipidomys mastacalis* were described by Zanchin et al. (1992).

[g] Modal counts from three specimens (AMNH 257274, MHNLS 7850, USNM 448625) karyotyped by RSV at San Ignacio Yuruaní, Estado Bolívar, Venezuela.

long, soft fur and a primitive carotid arterial circulation (pattern 1 of Voss, 1988); they occur in montane and premontane vegetation associated with rocky outcrops of the Pantepui complex (Tate, 1939; Handley, 1976; Gardner, 1989) and neither is known from French Guiana (where such habitats are absent). The other two species have shorter, coarser fur, a derived carotid arterial morphology (pattern 3 of Voss, 1988), and occur in lowland rainforest. One of the lowland rainforest species (represented by the Guianan holotypes of *sclateri* Thomas [1887], *bovallii* Thomas [1911b], and *aratayae* Guillotin and Petter [1984]) is large (HF = 32–36 mm; LM = 5.9–6.8 mm) with gray-based ventral fur, whereas the other (represented by the Guianan holotypes of *nitela* Thomas [1901], *fervidus* Thomas [1904], *milleri* Allen [1913b], and *yuruanus* Allen [1913b]) is small (HF = 24–28 mm, LM = 4.1–4.8 mm) with (usually) pure white ventral fur.

Although the oldest Guianan name for the large lowland species is *Rhipidomys sclateri,* Musser and Carleton (1993) and Tribe (1996) treated *sclateri* as a subjective junior synonym of *leucodactylus* Tschudi (1844), the type locality of which is in eastern Peru. Only a single specimen, the type of *R. leucodactylus aratayae,* is currently known from French Guiana.

The oldest Guianan name for the small lowland species is *Rhipidomys nitela,* but *nitela* has often been treated (e.g., by Cabrera [1961] and Husson [1978]) as a junior synonym of *R. mastacalis* (Lund, 1840), and some nominal taxa referable to *nitela* were originally described as subspecies of *R. venezuelae* Thomas (1896). Based on our examination of types and other material, we agree with Musser and Carleton (1993) and with Tribe (1996) that *nitela, mastacalis,* and *venezuelae* represent three valid species with diagnostic morphological and karyotypic attributes, and with discrete geographic ranges (table 37). Our six Paracou vouchers together with 13 additional specimens subsequently collected at Les Nouragues (by F. Catzeflis and his colleagues from Montpellier) are ap-

parently the only examples known from French Guiana.

For the most part, external and craniodental measurements of French Guianan specimens of *Rhipidomys nitela* agree closely with those of the Guyanese type series (table 38). Although relative tail length appears to be divergent in the two samples (averaging about 130% of head-and-body length in French Guianan material versus 115% in the type series), methodological artifacts might explain this proportional difference between small series of specimens measured in the field by different collectors. By contrast, measurements of the hindfoot and of the molars (both measured by us) suggest that the populations in question do not differ much, if at all, in size. Because the French Guianan material additionally resembles the type series in qualitative characters, we interpret these samples as representing populations of a single species.

Some of Husson's (1978: table 71) measurements of the hindfeet of Surinamese specimens that he identified as *Rhipidomys mastacalis nitela* are smaller than any that we or Tribe (1996) observed for this species. If Husson's material was correctly identified, which we do not doubt, it is likely that the feet were simply mismeasured. The single weight datum that Husson tabulated for this species (150 g) was obtained from a female with three near-term embryos and is obviously not comparable with our weights of nonpregnant animals.

All of the specimens that we refer to *Rhipidomys nitela* (see below) appear to represent a morphologically cohesive taxon that is geographically limited to the Guianan and Southeastern subregions of Amazonia. Tribe (1996), however, recognized two isolated records of *R. nitela* from outside Amazonia. One of these records, consisting of the type series of *R. nitela tobagi* Goodwin (1961) from Little Tobago Island, is equivocal in our judgment because the diagnostic presence of a conspicuous caudal tuft (fig. 61B) cannot be confirmed from the two partially decayed fluid specimens of this taxon; possibly, these represent an insular form of the adjacent mainland species *R. venezuelae*. The other nonAmazonian record of *R. nitela* mapped by Tribe (1996: fig. 7.6) is improbably isolated on the northern Caribbean coast of Colombia. We examined the voucher in question (MHNG 1706.75, from Bonda, Departamento Magdalena), which differs from *R. nitela* by its pale bicolored tail and short (6 mm) caudal tuft; in our opinion, this specimen represents another taxon, perhaps allied to *R. venezuelae* despite its short (4.6 mm) toothrow.

Recently, Anderson (1997) reported *Rhipidomys nitela* from eastern Bolivia, a considerable range extension that we attempted to confirm by examining his material. Of the two specimens that Anderson cited by number (AMNH 119406, UMMZ 156298), however, we were only able to locate one. That specimen, UMMZ 156298, is an example of *Thomasomys* resembling *T. oreas* Anthony (1926). Therefore, as far as we have been

TABLE 38

Measurements (mm) and Weights (g) of Adult *Rhipidomys nitela* from French Guiana and the Type Locality[a]

	French Guiana[b]	Quatatat, Guyana[c]
Sex	6 males, 4 females	4 males, 1 female
HBL	121 ± 9 (108–135) 9	122 (114–133) 5
LT	160 ± 9 (152–179) 9	140 (132–152) 5
HF[d]	26 ± 1 (24–28) 9	26 (25–27) 5
Ear	18 ± 1 (17–20) 9	17 (16–17) 5
CIL	28.2 ± 1.3 (26.5–30.3) 10	27.2 (26.1–29.2) 4
LD	8.2 ± 0.7 (7.4–9.3) 10	7.6 (7.2–8.2) 5
LM	4.5 ± 0.1 (4.3–4.6) 10	4.4 (4.2–4.7) 4
BM1	1.2 ± 0.0 (1.1–1.3) 10	1.2 (1.2–1.2) 5
LIF	6.3 ± 0.5 (5.5–7.1) 10	6.2 (5.7–7.0) 5
BIF	2.6 ± 0.2 (2.4–3.0) 9	—
BPB	3.2 ± 0.2 (2.9–3.8) 10	2.9 (2.7–3.0) 5
BZP	2.4 ± 0.2 (2.0–2.9) 10	2.3 (2.1–2.5) 5
LIB	5.3 ± 0.3 (5.0–5.8) 10	4.9 (4.5–5.2) 5
ZB	16.1 ± 1.2 (14.8–18.6) 10	15.5 (15.0–16.0) 3
Wt	56 ± 9 (44–68) 8	—

[a] Tabulated sample statistics include the mean ± one standard deviation, the observed range (in parentheses), and the sample size.

[b] Including Paracou vouchers: AMNH 267021, 267582, 267583, 269821; MNHN 1995.1012; V-831, -886, -890, -891, -893.

[c] The type series: BMNH 1.6.4.81–1.6.4.85. "Quatatat" is the spelling for the type locality inked on the skin labels, but Thomas (1901: 149) spelled it "Kwaimattat." Modern gazetteers (Stephens and Traylor, 1985) render this locality name as "Kwaimatta" with coordinates 3°49′N, 59°20′W.

[d] Remeasured from skins and fluid-preserved material.

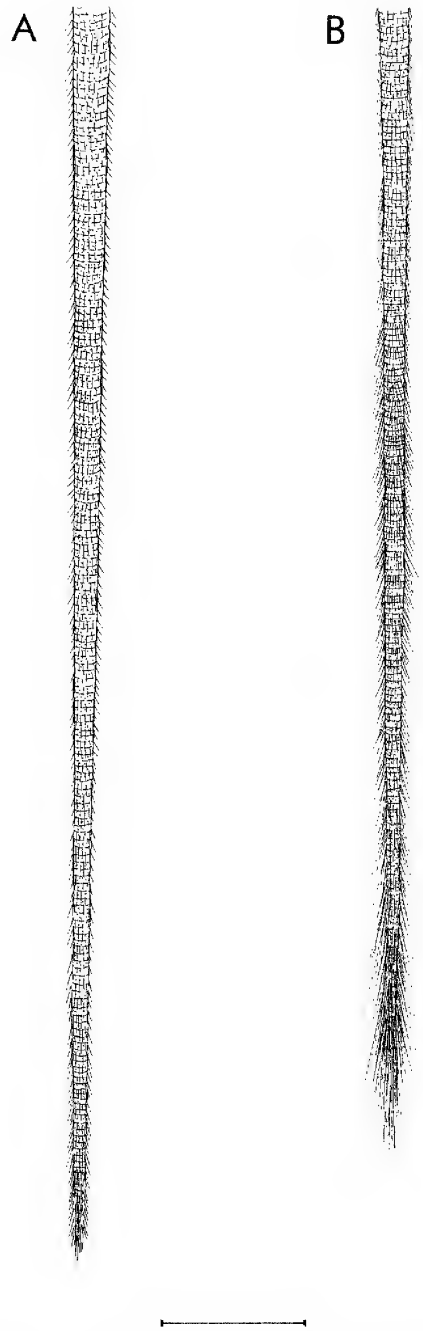

Fig. 61. Caudal morphology of *Rhipidomys venezuelae* (**A,** AMNH 131081) and *R. nitela* (**B,** AMNH 267021). The tail of *R. venezuelae* is uniformly covered by short hairs that are clearly visible without magnification but do not conceal the underlying epidermal scales; there is no terminal tuft of conspicuously longer hairs. By contrast, the caudal hairs of *R. nitela* increase in length from the base of that organ to the tip, where the longest hairs are concentrated to form a conspicuous terminal tuft. Scale bar = 20 mm.

able to determine by direct examination of museum specimens, *R. nitela* appears to be an Amazonian endemic that does not occur west of the north-south zoogeographic axis represented by the Rio Negro and the Rio Madeira.

Species of *Oecomys* externally resemble *Rhipidomys* by their large eyes, long vibrissae (extending well behind the pinnae when laid back alongside the head), short-broad hindfeet with semi-opposable fifth digits, and long tufted tails. At Paracou, *O. auyantepui* and *R. nitela* are of similar size and might be confused in the field. However, *R. nitela* and *O. auyantepui* differ in many external characters that are potentially useful for identification of specimens in hand. (1) Whereas the pinnae of *R. nitela* are blackish (contrasting in color with the fur of the head) and appear quite naked (a very sparse auricular pelage is visible only under magnification), the pinnae of *O. auyantepui* are not contrastingly colored and have a visible pelage of reddish-brown hairs. (2) The dorsal body pelage of *R. nitela* is very short (5–6 mm), somewhat coarse to the touch, and dull grayish-brown, but the dorsal fur of adult specimens of *O. auyantepui* is much longer (≥10 mm), very soft to the touch, and lustrous reddish-brown in appearance. (3) The ventral pelage of *R. nitela* is almost entirely self-colored (pure white or cream to the roots of the hairs), except immediately along the flanks (where some hairs have gray bases and white tips); by contrast, the ventral fur of *O. auyantepui* is mostly gray-based, except on the throat and along the midline (where some hairs are pure white). (4) The hindfeet of *R. nitela* are always prominently marked by a dark band of brownish hairs that extends from the ankle over all or part of the metatarsus to the base of the toes, which are usually white (pigmented hairs extend onto the proximal phalanges of the middle toes in a few specimens, but the outermost digits are always completely white); by contrast, pedal markings are not conspicuous in most specimens of *O. auyantepui,* some of which have uniformly pale feet. (5) Adult female specimens of *Rhipidomys* have six mammae in postaxial, abdominal, and inguinal pairs (muroid mammary loci are illustrated in Voss and Carleton, 1993: fig. 8), but female *Oecomys* have

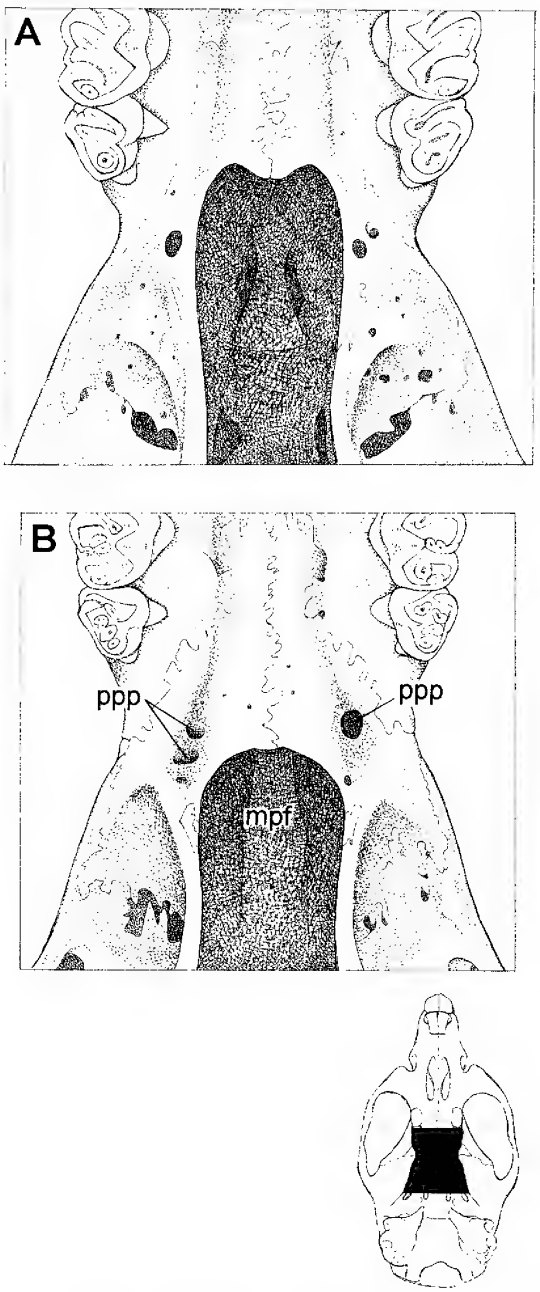

Fig. 62. Posterior palatal morphology of *Rhipidomys nitela* (**A,** AMNH 267582) and *Oecomys auyantepui* (**B,** ROM 103244). In *Rhipidomys* (and other "thomasomyines"; see Voss, 1993), the palate is said to be "short" because the mesopterygoid fossa (**mpf**) extends anteriorly to or between the last molars; additionally, posterolateral palatal pits (**ppp**) are small or absent in "thomasomyines". By contrast, the palate of *Oecomys* and other oryzomyines is said to be "long"

eight mammae (the additional teat-pair is pectoral).

Extended craniodental comparisons between *Rhipidomys* and *Oecomys* are unnecessary for fieldworkers, but it is relevant to note that these genera superficially resemble one another by their shallow zygomatic notches, convergent and beaded supraorbital margins, and pentalophodont molars. Nevertheless, skulls found in stomachs or scat can be easily identified by palatal architecture. The bony palate of *Rhipidomys* (fig. 62A) is "short" because it does not extend behind the molar rows, and the posterior palatal margin is biconcave because a small median palatal process is present; the posterior palatal pits are small, simple perforations. By contrast, the bony palate of *Oecomys* (fig. 62B) is "long" (extending behind the molar rows) with a typically arch-shaped posterior margin, and the posterior palatal pits are larger and often more complex. The only French Guianan species of *Rhipidomys* and *Oecomys* that are at all likely to be confused, *R. nitela* and *O. auyantepui,* can also be distinguished by carotid arterial morphology (pattern 3 versus pattern 1 [of Voss, 1988], respectively), but carotid morphology does not consistently differ between other representatives of these genera.

Other Specimens Examined: **Brazil**—*Pará,* Aramanay on Rio Tapajos (AMNH 94810–94813). **French Guiana**—Les Nouragues (AMNH 269821; V-824, −825, −826, −831, −876, −886, −890, −891, −893, −905, −914). **Guyana**—*Potaro-Siparuni,* Minnehaha Creek (AMNH 36331–36336 [type series of *milleri*]); *Upper Takutu-Upper Essequibo,* Quatatat (BMNH 1.6.4.81–1.6.4.86 [type series of *nitela*]). **Venezuela**—*Bolívar,* La Unión (BMNH 4.5.7.34, 4.5.7.35 [type series of *fervidus*]), La Vuelta (BMNH 4.5.7.36), Río Yuruán (AMNH 30727–30735, 30737 [type series of *yuruanus*]), San Ignacio Yuruaní (AMNH

←

because the mesopterygoid fossa does not extend anteriorly to the last molars; also, the posterolateral palatal pits of oryzomyines are large, sometimes complex, and frequently recessed in shallow fossae.

257273–257275; MHNLS 7845, 7846, 7848–7850, 7891, 7892, 7895, 7896, 7898, 7899, 8072, 8074; USNM 448613–448616, 448618–448623, 448625–448628).

FIELD OBSERVATIONS: All of our definite records of *Rhipidomys nitela* at Paracou are based on collected specimens. In 1992, one adult female was shot in the daytime as it perched several meters above ground level in the dark interior of a hollow tree (fig. 63). In 1993, the same tree cavity contained four individuals, of which one adult female and two juveniles were shot and one juvenile escaped. One specimen was captured at ground level in a pitfall, and two others were taken in platform traps 14.5–15.2 m above the ground. All of our vouchers were shot or trapped in well-drained primary forest.

ERETHIZONTIDAE

Coendou melanurus (Wagner)

Figures 64, 65, 67, 68, 69, 70A, 71

Only two specimens documented the occurrence of this distinctive porcupine in French Guiana prior to fieldwork at Paracou: the mounted skin of an immature animal from "Guyane" (MNHN 1909.241), and an adult skin-and-skull from St. Laurent du Maroni (MNHN 1909.242). Just a single individual (AMNH 266565) was encountered in our inventory, but simultaneous faunal rescue operations at the Petit Saut hydroelectric dam site resulted in 59 captures (Lemercier, 1998; Vié, 1999), from which three specimens were salvaged as vouchers (MNHN 1997.640, 1997.641, 1999.1080; F. Catzeflis, personal commun.). Evidently, the species is not rare, but cryptic. Because the morphological and geographic limits of *Coendou melanurus* are not adequately documented in the literature, we redescribe the species below, discuss its morphological variation, compare it with other congeners, and provide new information about its geographic range.

TYPE MATERIAL: Wagner's (1842) original material of *Cercolabes melanurus* consists of two specimens in the Naturhistorisches Museum Wien collected by Johann Natterer at Barra do Rio Negro (= Manaus), Estado Amazonas, Brazil.[19] Both are skins, originally stuffed and mounted for exhibition, with skulls and mandibles subsequently extracted.

In order to clarify the application of *Cercolabes melanurus,* we select as lectotype NMW 42010, an adult female collected in February 1834. The skull (fig. 64) is that of a fully mature animal, with slightly swollen frontal sinuses and most cranial sutures fused; the cheekteeth are worn flat, but all essential details of the occlusal morphology remain. The squamosal root of the right zygomatic arch is broken, as is the right pterygoid process; both occipital condyles and part of the basioccipital are missing. The skin (fig. 65) is essentially intact, but the tail is partially broken away at the base and secured to the body with thread. The paralectotype (NMW B-1017) is a subadult female with deciduous premolars and unfused cranial sutures. Like the lectotype, the tail of this specimen is partially broken away and tied to the body with thread.

DISTRIBUTION: Specimens that we examined and literature records that we judge to be reliable suggest that *Coendou melanurus* ranges throughout the Guiana subregion of Amazonia (fig. 66). Although Emmons (1990, 1997), Alberico et al. (1999), and Tirira (1999) described the range of *C. melanurus* as extending into western Amazonia, all extralimital records that we investigated were found to be based on misidentified material of other species (see Comparisons, below).

DESCRIPTION: Small long-tailed porcupines (see measurements in table 39) with dorsal pelage composed of short quills more-or-less concealed beneath a thick coat of long blackish fur coarsely streaked with yellow. Quills bicolored (yellowish basally with dark-brown tips), about 3 cm or less in length, densely covering dorsal surface of head, neck, trunk, and upper limbs, but only exposed on cheeks and crown of head (except where fur has come away in patches due to

[19] A third specimen in the same museum (NMW B-1006), consisting of a stuffed skin with skull and mandibles inside, lacks locality information and is not part of Natterer's collection from Barra do Rio Negro (Pelzeln, 1883). According to the museum's acquisition catalogs and card files, NMW B-1006 was purchased in London by L. v. Fichtel in 1809 and may have originated from the Guianas (K. Bauer, personal commun.).

Fig. 63. Diurnal refuge of *Rhipidomys nitela* at Paracou. Specimens were collected in 1992 and 1993 from the dark internal cavity (arrow) of this large kimboto (Sapotaceae: *Pradosia cochlearia*), a canopy emergent in well-drained primary rainforest.

Fig. 64. Dorsal, ventral, and lateral cranial views of NMW 42010, lectotype of *Coendou melanurus* (Wagner). All views approximately ×1.3.

Fig. 65. Dorsal and ventral views of the skin of NMW 42010, lectotype of *Coendou melanurus* (Wagner). Both views approximately ×0.5.

faulty preservation). Dorsal fur long and abundant, concealing quills from crown to rump; individual hairs pale basally (among the quills), but emergent fur black heavily streaked with pale yellow (a mass effect produced by coarse guard hairs with very long yellow tips scattered abundantly among finer hairs that are entirely black or have only inconspicuous pale tips). Ventral surface of body without offensive quills, covered

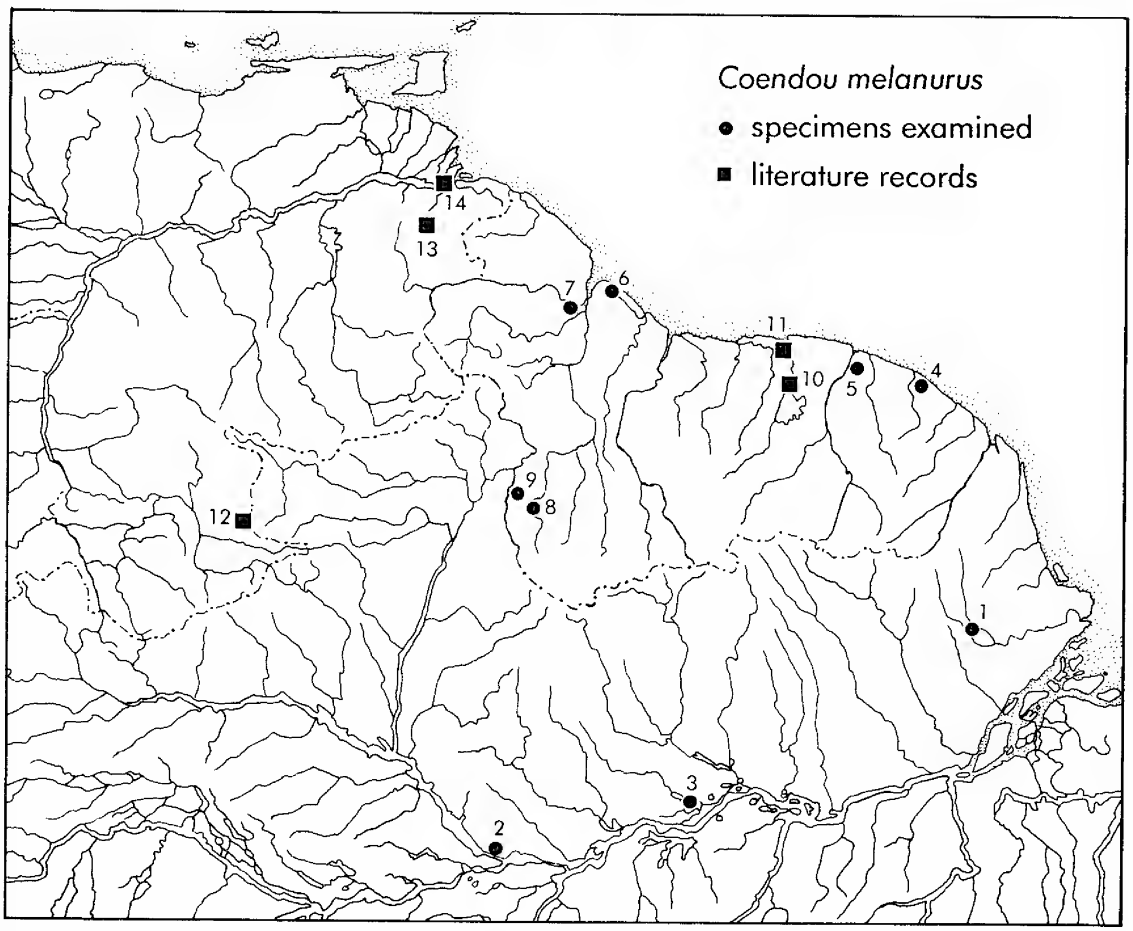

Fig. 66. Geographic range of *Coendou melanurus* based on specimens examined and literature records. **1,** BRAZIL, *Amapá,* Serra do Navio; **2,** BRAZIL, *Amazonas,* Manaus; **3,** BRAZIL, *Pará,* Lago Claimy; **4,** FRENCH GUIANA, Paracou; **5,** FRENCH GUIANA, St.-Laurent du Maroni; **6,** GUYANA, *Demerara-Mahaica,* Georgetown; **7,** GUYANA, *Cuyuni-Mazaruni,* Kartabo; **8,** GUYANA, *Upper Takutu-Upper Essequibo,* 25 mi E Dadanawa; **9,** GUYANA, *Upper Takutu-Upper Essequibo,* Nappi Creek; **10,** SURINAM, *Brokopondo,* Afobaka (Husson, 1978); **11,** SURINAM, *Suriname,* Paramaribo (Husson, 1978); **12,** VENEZUELA, *Amazonas,* Sierra Parima (Linares, 1998); **13,** VENEZUELA, *Bolívar,* Imataca (Ochoa, 1995); **14,** VENEZUELA, *Delta Amacuro,* Delta del Orinoco (Linares, 1998).

sparsely with short, coarse, brownish hairs (usually frosted with whitish bands or tips) from chin to anus. Face with very short quills on forehead and cheeks but otherwise almost naked, especially around eyes; facial vibrissae consisting of long, black mystacial, genal, and superciliary hairs; submental vibrissae short and black. Pinnae rudimentary and almost naked. Hands and feet covered dorsally with very coarse blackish hairs. Tail probably about as long as head-and-body on average; dorsum of proximal third with body pelage (quills and yellow-streaked black fur), but remainder of tail (except for naked prehensile surface) densely covered above and below with stiff black bristles.

Frontal and nasal sinuses uninflated (resulting in a flattened dorsal profile from midparietal region to nasal tips) or weakly inflated (resulting in a noticeable bulge over the orbits). Rostrum usually short and very broad, not conspicuously excavated laterally for origin of infraorbital muscle; nasals parallel-sided or weakly convergent posteriorly, with rounded posterior margins that extend well behind the premaxillae. Zygomatic

TABLE 39
Measurements (mm) of *Coendou melanurus*

	Adults			
	Paracou voucher[a]	Lectotype[b]	Other specimens[c]	Subadults[d]
Sex	male	female	2 males, 3 females	6 females
HBL	424	—	385 (330–415) 5	365 (330–435) 5
LT	415	—	373 (340–415) 5	399 (356–455) 5
HF	73	—	70 (65–82) 4	72 (65–82) 5
CIL	76.5	—	75.3 (70.6–78.1) 5	73.1 (69.4–79.3) 6
LD[e]	21.1	22.9	19.8 (17.4–21.3) 5	[19.6 (18.0–22.3) 6]
MTR[e]	17.5	19.4	17.2 (15.7–17.9) 5	[17.0 (16.4–18.2) 6]
LM	13.2	14.4	12.7 (11.5–13.2) 5	13.2 (12.9–14.1) 6
BM1	4.6	4.5	4.5 (4.3–4.8) 5	4.6 (4.4–4.8) 6
BPB	4.4	4.2	4.9 (4.3–5.5) 5	5.0 (4.3–5.4) 6
ZB	43.2	46.3	44.6 (41.4–47.2) 5	43.0 (39.9–46.6) 6
ZL	27.3	31.7	29.2 (26.8–31.1) 5	28.7 (25.8–32.3) 6
LN	26.7	27.8	24.4 (22.4–26.0) 5	24.8 (23.5–25.6) 4
BB	35.2	33.0	33.8 (32.3–34.8) 5	33.0 (31.0–37.3) 6

[a] AMNH 266565.

[b] NMW 42010, as designated in this report (see text).

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 70120, 70131, 94174, 142955; FMNH 17762.

[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: NMW B-1017; ROM 31683, 31783, 31801, 31984; USNM 394732.

[e] Measurements of subadults (in square brackets) have dP4 rather than P4 as one endpoint.

arches (viewed from above) usually with rounded lateral deflection at orbits, but sometimes convergent anteriorly with no orbital deflection (e.g., AMNH 266565); jugals moderately expanded dorsoventrally behind maxillary suture. Dorsolateral contours of braincase weakly sculpted by bony scars of M. temporalis in most specimens (but temporalis scars well marked in AMNH 70120), the right and left scars always widely separated (never joined to form a sagittal ridge or crest).

Incisive foramina short and completely contained by premaxillae (e.g., AMNH 94174), or longer and bordered by maxillae posteriorly; left and right foramina recessed in a common fossa and incompletely separated (e.g., AMNH 94174) or completely separated by a stout bony septum and not recessed (e.g., AMNH 142955). Posterior diastema usually distinctly trisulcate; palatal bridge usually without a distinct median keel, or keel weakly developed (never a high crest flanked by deep lateral gutters). Anterior margin of mesopterygoid fossa a broad, blunt wedge penetrating between third molar crowns; bony roof of mesopterygoid fossa usually completely ossified (sometimes with tiny perforations but never large vacuities). Auditory bullae very large and antero-posteriorly elongated; roof of external auditory meatus with conspicuous bony ridge extending from dorsal lip of bulla to malleus.

VARIATION: This species is extraordinarily uniform in qualitative external characters despite the apparent plasticity of some morphometric and osteological traits. High variability in external measurements (table 39) is common in erethizontids because of the difficulty of handling animals protected by sharp quills; additionally, porcupine feet do not resemble those of other rodents, and some field collectors may have measured the hindfoot erroneously, from the rounded posterior margin of the plantar callosity instead of the heel. As in other caviomorphs, qualitative cranial and dental characters of erethizontids are annoyingly variable. Some differences among the specimens of *Coendou melanurus* that we examined may be corre-

lated with age and sex, but with miniscule samples from widely scattered localities, interpretation is difficult.

COMPARISONS: Many faunal accounts and checklists (e.g., Cabrera, 1961; Husson, 1978; Woods, 1993) have treated *Coendou melanurus* as a subjective junior synonym of *C. insidiosus* (Olfers, 1818), a taxon endemic to the Atlantic rainforests of southeastern Brazil. The history of this erroneous usage was reviewed by Voss and Angermann (1997), who rediscovered and redescribed the holotype of *C. insidiosus,* compiled geographic data from other known specimens, and provided diagnostic comparisons with *C. melanurus.* Morphological differences between these highly distinctive species are here illustrated for the first time (figs. 67–70).

Other species of South American porcupines with long fur are easily distinguished from *Coendou melanurus* by conspicuous external characters. For example, *Coendou vestitus* Thomas (1899c) and *C. pruinosus* Thomas (1905) from Venezuela and Colombia are smaller, shorter-tailed porcupines that have long wire-like bristles mixed among the quills and woolly fur of the dorsal pelage. We have also examined several Ecuadorean specimens previously misidentified as *C. melanurus* and determined that they represent an undescribed species of the *vestitus* group; this taxon superficially resembles *melanurus* because it has long yellow-tipped bristles that contrast with the black-tipped quills to produce a similarly streaked pelage pattern. However, the new species is substantially smaller (HF, 58–59 mm; CIL, 58.8–64.4 mm; MTR, 14.1–15.2 mm), lacks a dense coat of long adult fur, and has more acutely angled mesopterygoid margins that penetrate more deeply between the toothrows (Voss and da Silva, submitted).

Throughout the Guiana subregion of Amazonia, *Coendou melanurus* is sympatric with another congener, *C. prehensilis* (see below). Although *melanurus* is smaller than *prehensilis,* there is some overlapping variation in weights and linear dimensions from large sympatric samples (Richard-Hansen et al., 1999). Fortunately, the two species are unmistakeable in qualitative external characters (fig. 71). Diagnostic craniodental comparisons between Surinamese samples of *melanurus* and *prehensilis* were discussed by Husson (1978), who misidentified his material of the former species as *Sphiggurus insidiosus* (see above and Remarks, below)

REMARKS: *Coendou melanurus* and other long-furred Neotropical porcupines have often been referred to the genus *Sphiggurus* F. Cuvier (most recently by Husson, 1978; Concepción and Molinari, 1991; Woods, 1993; Eisenberg and Redford, 1999). However, we agree with Handley and Pine (1992) that *Coendou* and *Sphiggurus* are not meaningfully diagnosable based on current knowledge of morphological character variation, and that the latter name should be treated as a subjective junior synonym of the former.

Sphiggurus melanurus Gray (1842), published in the same year as *Cercolabes melanurus* Wagner, is based on a skin in the Natural History Museum (London) bearing the number 86a on a cardboard tag attached to the hindfoot. This specimen agrees in every essential respect with Wagner's type series and with the other material herein referred to *Coendou melanurus.* Waterhouse (1848: 425), the first reviser in the sense of the International Code of Zoological Nomenclature (ICZN, 1999), can be considered to have chosen Wagner's name to have precedence over Gray's (a junior subjective synonym).

SPECIMENS EXAMINED: **Brazil**—"Brazil" (BMNH specimen numbered 86a in J. E. Gray's manuscript catalog [type of *melanurus* Gray]); *Amapá,* Serra do Navio (USNM 394732); *Amazonas,* Manaus (NMW 42010, B-1017); *Pará,* Lago Claimy on Rio Jhamunda (AMNH 94174). **French Guiana**—"Guyane" (MNHN 1909.241), Paracou (AMNH 266565), St.-Laurent du Maroni (MNHN 1909.242). **Guyana**—*Cuyuni-Mazaruni,* Kartabo (AMNH 70120, 70131, 142955); *Demerara-Mahaica,* Georgetown (FMNH 17762); *Upper Takutu-Upper Essequibo,* 25 mi E Dadanawa (ROM 31984), Nappi Creek near Letham (ROM 31683, 31783, 31801). **No locality data**—(NMW B-1006).

FIELD OBSERVATIONS: Our single voucher is the only definite record we have of *Coendou melanurus* from Paracou; surprisingly, none of the forestry personnel whom we in-

Fig. 67. External morphology of *Coendou melanurus* (left, AMNH 266565) and *C. insidiosus* (right, AMNH 90119). Although these species are similar in possessing short bicolored quills concealed by long fur, *C. melanurus* has a much longer tail relative to head-and-body length, and its coarse blackish dorsal fur is heavily streaked with yellow- or white-tipped guard hairs; the caudal bristles (covering the tail between its furry base and naked prehensile tip) are jet black. By contrast, *C. insidiosus* is relatively shorter-tailed and has softer smoky-gray (or whitish) dorsal fur without contrastingly colored guard hairs; the caudal bristles are brownish, not black. Both views approximately ×0.3.

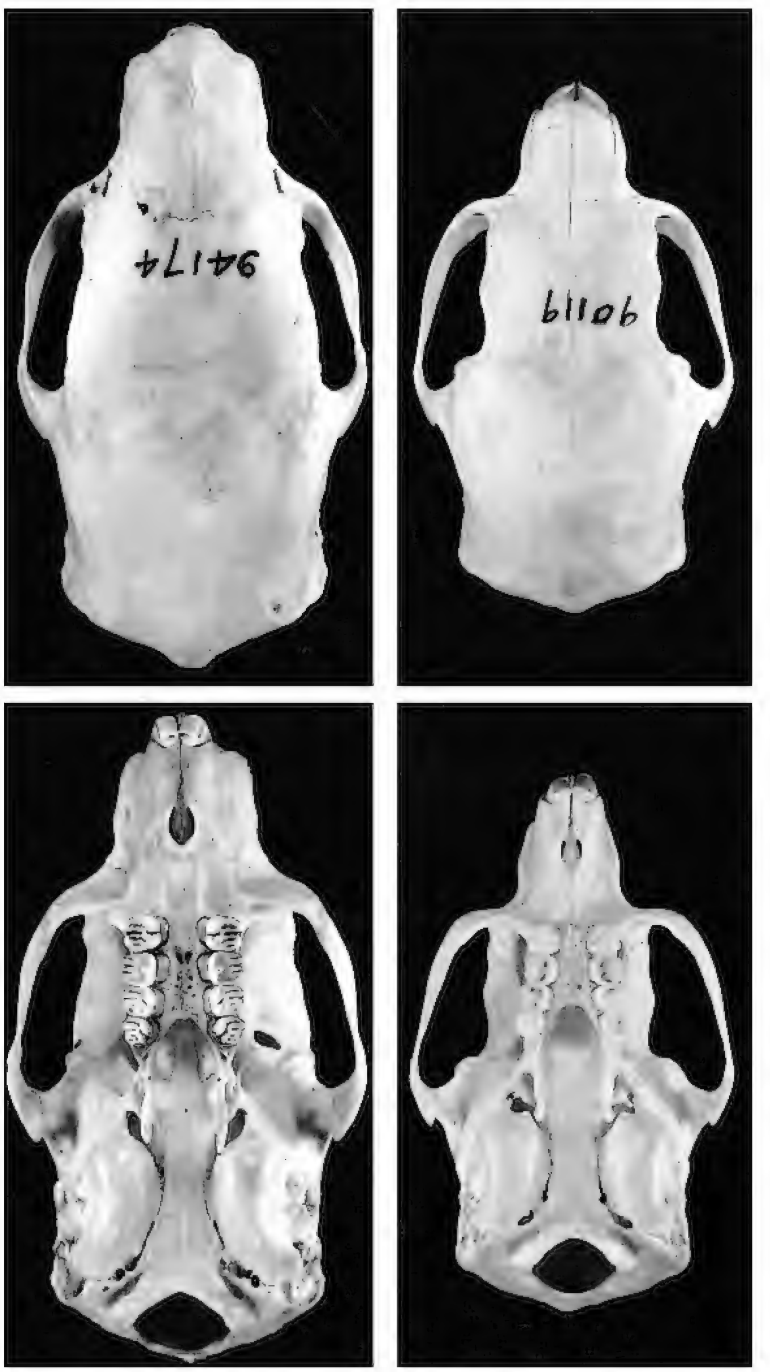

Fig. 68. Dorsal and ventral cranial views of *Coendou melanurus* (left, AMNH 94174) and *C. insidiosus* (right, AMNH 90119). All views approximately life-size.

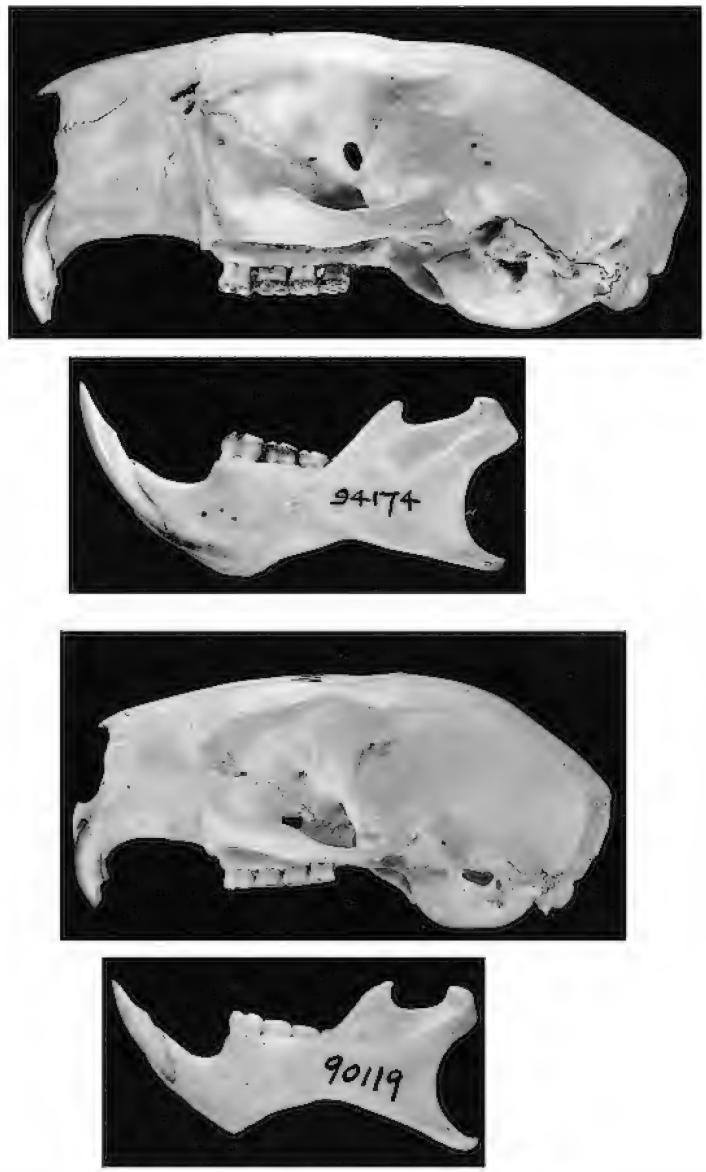

Fig. 69. Left lateral cranial views of *Coendou melanurus* (top, AMNH 94174) and *C. insidiosus* (bottom, AMNH 90119). All views approximately life-size.

terviewed were aware that this species occurred in the area. This specimen was shot at night as it perched 15–20 m above the ground in the subcanopy of well-drained primary forest; its stomach was completely filled with a homogeneous, finely masticated, bright-green pulp. We surmise that the animal had been eating the new leaves of the tree in which it was shot because these had the same color and odor when crushed as the freshly dissected stomach contents.

Coendou prehensilis (Linnaeus)

Figure 71

Although we did not directly observe this species at Paracou, we found one of its distinctively large, tricolored quills on a dirt road near our camp. P. Petronelli (personal

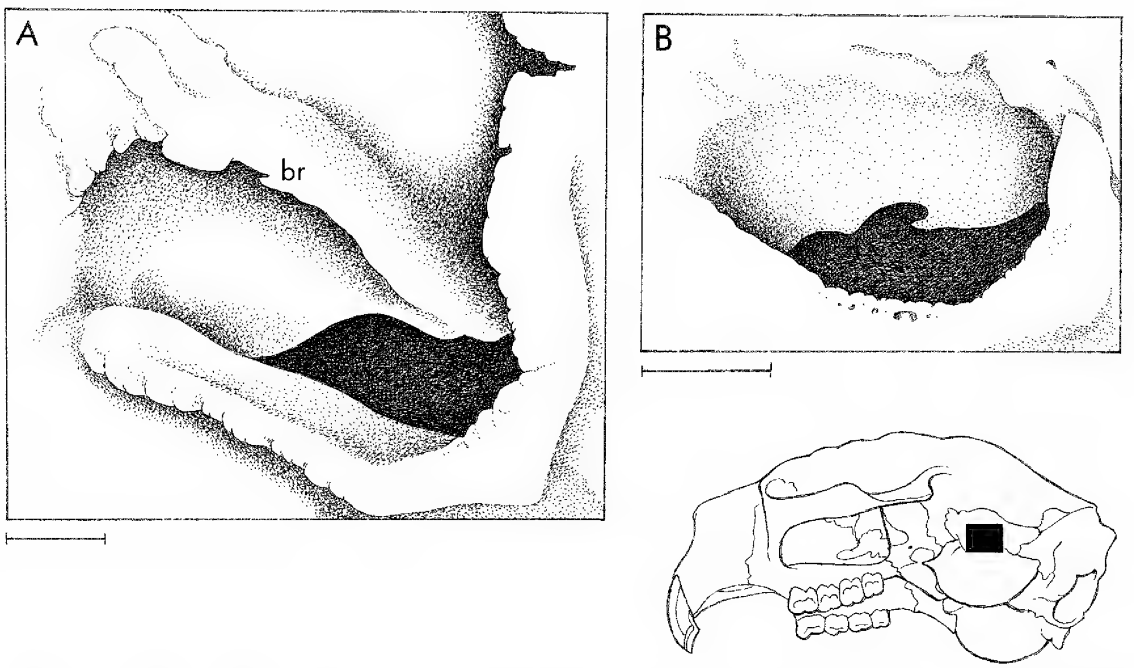

Fig. 70. Morphology of the roof of the external auditory meatus in *Coendou melanurus* (**A,** AMNH 266565) and *C. insidiosus* (**B,** AMNH 90119). In *C. melanurus,* the roof of the meatus has a prominent bony ridge (**br**) that is lacking in *C. insidiosus.* Scale bars = 1 mm.

commun., 1993) told us that he had also found quills of this species lying on the ground in our study area, and that an ocelot (*L. pardalis*) killed at Paracou by a local hunter several years before our inventory work began had quills of *C. prehensilis* embedded in its neck and shoulders. The species has occasionally been observed in roadside secondary growth by visiting researchers (G. Dubost, personal commun.), but accurate counts of such observations are unavailable.

Dasyproctidae

The Paracou fauna contains two dasyproctids, one species each of *Dasyprocta* and *Myoprocta,* the usual number known to occur sympatrically throughout most of Amazonia. Although Guianan dasyproctids are easily identified in the field and in the museum, their technical names are still controversial due to unresolved issues of usage and synonymy. Large, edible, and diurnal, dasyproctids were among the first mammals of the Guianan fauna to be reported by European travellers, whose inadequate published descriptions are at the root of several nomenclatural problems.

Dasyprocta leporina (Linnaeus)

Voucher Material: AMNH 265955; MNHN 1998.677. Total = 2 specimens.

Identification: The genus *Dasyprocta* has never been revised and the current species-level taxonomy (e.g., as summarized by Cabrera, 1961; Emmons, 1990, 1997; Woods, 1993) is sorely in need of critical attention. Traditionally, the red- or yellow-rumped agoutis of Amazonia have been referred to *D. aguti* (Linnaeus, 1766), but the oldest available name for these animals is unequivocally *D. leporina* (Linnaeus, 1758) (see Husson [1978] and Remarks, below).

Our voucher material closely resembles Husson's (1978) description of *Dasyprocta leporina,* which was based on the neotype and other specimens from Surinam. The only noteworthy point of difference is the color of the long nape hairs, which are blackish in our vouchers, whereas Husson (p. 459) stated that "[t]he anterior part of the dorsal surface

Fig. 71. Unvouchered photographs of living *Coendou melanurus* (top) and *C. prehensilis* (bottom, not to same scale) from Petit Saut, French Guiana (ca. 28 km SSW Paracou). Both animals are alarmed, so the pale bases of their erected quills are exposed. When *C. melanurus* is not alarmed and defensive, its short bicolored (black-tipped) quills are hidden beneath a dense coat of long fur (see fig. 67). By contrast, the large tricolored (white-tipped) quills of *C. prehensilis* are always visible because the short sparse fur of this species is concealed among the quill bases. Also note the diagnostically bulging forehead and swollen muzzle of *C. prehensilis,* and the equally diagnostic blackish caudal bristles of *C. melanurus.* From color transparencies by J.-C. Vié.

of the body including the neck is olivaceous gray speckled with yellowish", the nuchal hairs apparently not being distinctively colored in the neotype. Husson's other specimens, however, were described (op. cit.) as having darker necks, and most of the Surinamese agoutis we examined had blackish napes like our vouchers. As noted by Husson, the rump color in this species is also variable, ranging from clear yellow-orange to grizzled reddish-brown in the specimens we examined. Although our single adult voucher (AMNH 265955) is larger than any of the 12 Surinamese specimens measured by Husson (1978: table 82), the differences between homologous dimensions of AMNH 265955 and his largest example (RMNH 18235) are proportionately small (e.g., about 4% in maxillary toothrow length), and we do not regard them as taxonomically significant. Morphometric variation among nine FMNH specimens from Surinam (table 40) likewise suggests that our voucher is large but probably not outside the normal size range of typical *D. leporina.* For future revisionary work, a large series of specimens collected by H. A. Beatty in the Wilhelmina Mountains of Surinam (see Specimens Examined, below) provides a useful sample of individual variation from a single local population of this nomenclaturally important species.

TABLE 40
Measurements (mm) and Weights (kg) of *Dasyprocta leporina* from French Guiana and Surinam

	Paracou voucher[a]	Neotype[b]	Other Surinamese specimens[c]
Sex	male	female	7 females, 2 males
HBL	644	565	557 (515–595) 8
LT	26	30	23 (18–27) 8
HF	148	140[d]	142 (125–155) 8
Ear	46	46	50 (45–54) 8
CIL	112.3	—	104.9 (96.5–111.5) 9
LD[e]	34.6	30.5	30.8 (27.0–32.1) 9
MTR[e]	23.1	21.5	22.0 (19.6–24.3) 9
LIF	4.9	8.7	5.7 (4.5–7.9) 9
BIF	3.8	3.8	3.7 (2.9–4.5) 9
LN	52.8	—	47.0 (41.5–50.6) 9
LIB[f]	31.1	32.0	32.4 (29.3–34.4) 9
ZL	31.4	—	31.2 (29.4–33.1) 9
ZB	55.1	52.2	53.3 (50.8–56.8) 9
Wt	5.1	4.5	—

[a] AMNH 265955.
[b] RMNH 20752; measurements from Husson (1978: table 82).
[c] The sample mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: BMNH 52.1152–52.1156; FMNH 95765, 95767, 95769–95771, 95774.
[d] Without claws.
[e] Alveolar measurements.
[f] Measured between supraorbital notches.

Both Cabrera (1961) and Ojasti (1972) recognized several subspecies of *Dasyprocta aguti* (= *D. leporina*; see above and Remarks, below) as valid, but the necessity for a trinomial classification remains to be convincingly established by a comprehensive study of geographic variation. From the close similarity between our voucher material and the Surinamese specimens with which we compared them, the Paracou population would be unambiguously referable to the nominate form if other subspecies were to be recognized in a future revisionary study. Alternatively, it is possible that red-rumped agoutis include two or more separate species (as suggested by Krumbiegel, 1941), another hypothesis that remains to be effectively tested by critical analyses of specimen data.

The type of *Dasyprocta cristata* (Geoffroy, 1803) and another specimen so identified in the RMNH are both zoo animals said to have been collected in Surinam (Husson, 1978). A single 19th-century RMNH specimen of *D. fuliginosa* is also said to have come from Surinam (op. cit.). None of this material, however, is accompanied by names of collectors, dates of collection, or any additional geographic information. Because we have not seen any material referable to *D. cristata* or *D. fuliginosa* accompanied by definite evidence of origin from any of the Guianas, we assume that these old and poorly documented Surinamese records are erroneous. As discussed by Goeldi and Hagmann (1904), Thomas (1917), and Cabrera (1961), the type of *D. prymnolopha,* said to be from "Guiana" (Wagler, 1831: 619), was probably collected somewhere along the Atlantic coast of Brazil between the mouth of the Rio Tocantins and Bahia. Apparently, *D. leporina* is the only agouti species validly known from Guyana, Surinam, French Guiana, and Guianan Brazil. The black agouti (*Dasyprocta fuliginosa*), however, occurs allopatrically

in the headwaters of the Orinoco (geographically part of the Guiana subregion of Amazonia) in southernmost Amazonian Venezuela (Tate, 1939; Ojasti, 1972; Handley, 1976).

REMARKS: Although *Dasyprocta aguti* has long been used as the technical name for one or more geographic forms of red- or yellow-rumped agoutis (e.g., by Waterhouse, 1848; Thomas, 1917; Cabrera, 1961), the basis for this traditional usage is problematic. Because Linnaeus's (1766) original description of *Mus aguti* did not mention rump color, the identification of *aguti* has been justified primarily by reference to the bibliographic sources of his account (Marcgraf, 1648; Piso, 1658; Ray, 1693; Brisson, 1756). Thomas (1898) argued that all of Linnaeus's sources for *Mus aguti* could be traced back to the Brazilian animal described by the Dutch explorer-naturalist Georg Marcgraf. According to Thomas, Marcgraf's agouti was a yellow-rumped animal, but this inference is not consistent with what is known about the South American travels of that author.

Marcgraf, an employee of the Dutch West India Company, principally resided at Recife in the northeastern state of Pernambuco, from which base he explored the region effectively controlled by the 17th-century Dutch millitary occupation of northeastern Brazil (Whitehead, 1979). However, red- (or yellow-) rumped agoutis are not known to occur in Pernambuco (see range map in Emmons, 1990, 1997), nor anywhere else within the geographic limits of Dutch Brazil (as mapped by Boxer, 1973). Instead, Marcgraf's agouti was almost certainly the black-rumped species of the northeastern Brazilian coast, a taxon currently known as *D. prymnolopha* (Wagler, 1831). Marcgraf's (1648) brief color description and an accompanying woodcut of his "Aguti vel Acuti Brasiliensibus" are too ambiguous to support or refute this inference, but a painting by one of Marcgraf's contemporaries in Dutch Brazil (reproduced by Teixeira, 1995: vol. 5, p. 28) shows the local species as a more-or-less reddish animal with a blackish middorsal stripe over the rump, closely resembling *D. prymnolopha* of current usage.

Although this line of reasoning suggests that *Dasyprocta aguti* is a senior synonym of *D. prymnolopha* (as suggested by Carvalho and Toccheton, 1969) and not a junior synonym of *D. leporina* (contra Husson, 1978), our examination of Linnaeus's (1766) bibliographic sources for *Mus aguti* does not support Thomas's (1898) statement that all were based on Marcgraf's species. Whereas it is true that Piso's (1658: 102) and Ray's (1693: 226) accounts were obviously extracted from Marcgraf (1648), Brisson's (1756: 143) agouti description was based on an examined specimen (as previously noted by Tate, 1935). Unfortunately, Brisson's description is taxonomically uninformative (like Marcgraf's), and the geographic origin of his specimen is not stated. However, Brisson was employed in the natural history cabinet of the French naturalist Réaumur (Taton, 1970), so it is probable that all of the Neotropical specimens seen by him were from French Guiana. Additionally, Brisson (1756: 144) gave the geographic range of his agouti as "Guiania & Brasilia" and he cited Barrère's (1741) description of the "Agouty" of Cayenne. After Réaumur's death, his collection was transferred to the Cabinet du Roi (Taton, 1970), which subsequently became part of the Muséum National d'Histoire Naturelle. Geoffroy (1803), however, recorded no MNHN agouti material from the "ancien cabinet", nor does that museum now contain any 18th-century specimen of *Dasyprocta* that might have been the one described by Brisson (L. Granjon, personal commun.).

Finally, Linnaeus's (1766: 80) account of *Mus aguti* gave the geographic range as "Brasilia, Surinamo, Guiania" despite the fact that none of his cited references for this species mentioned Surinam. It is therefore probable that Linnaeus himself either had seen specimens of Surinamese agoutis or had reliable reports of them from his many Dutch colleagues and aquaintances. Regrettably, no material of *Dasyprocta* that is certainly known to have been examined by Linnaeus has apparently been identified in the literature, nor have we succeeded in locating any nomenclaturally useful 18th-century specimens in museums known to contain Linnaean mammals. However, any Surinamese agoutis seen by or reported to Linnaeus were necessarily red-rumped animals.

Linnaeus's *Mus aguti* is therefore composite, having been based directly or indirectly

on lost specimens of both the red- and the black-rumped species. Because Thomas's (1898) proposal to restrict *aguti* to Marcgraf's Brazilian animal was not equivalent to a lectotype designation, the application of the name *aguti* is still an open question. In our judgment, it would not be desirable to replace *prymnolopha,* the name by which the black-rumped agouti of the Brazilian Atlantic coast has been long and consistently known, with *aguti,* the traditional name for the red-rumped species. We therefore select as the neotype for *Mus aguti* Linnaeus (1766) the same specimen (RMNH 20752) that Husson (1978) designated as the neotype of *Mus leporinus* Linnaeus (1758). By this action *Dasyprocta aguti* becomes an objective junior synonym of *D. leporina* and current usage (Woods, 1993) is preserved.

Other Specimens Examined: **Surinam**—*Brokopondo,* Locksie Hattie on the Saramacca River (FMNH 95757, 95758, 95760); *Marowijne,* Paloemeu Camp (FMNH 95763, 95765, 95767–95771); *Nickerie,* Wilhelmina Mountains on West River (FMNH 95772–95778, 95790–95792); *Para,* Zanderij (BMNH 1952.1152–1952.1154); *Paramaribo,* Paramaribo (BMNH 1952.1155, 1952.1156); *Saramacca,* Dirkshoop (FMNH 95761); *Suriname,* Carolina Kreek (FMNH 95756).

Field Observations: We saw or heard *Dasyprocta leporina* almost every day that we were in the forest at Paracou, often in the early morning or late afternoon, less frequently in the middle of the day, and only rarely after dark (most nocturnal sightings may have been of individuals frightened from their resting places in dense vegetation). Most individuals were encountered singly, but a few groups of two or three individuals were also seen. We recorded sightings in well-drained primary forest, swampy primary forest, creekside primary forest, and roadside secondary growth. Both of our voucher specimens were shot.

Myoprocta acouchy (Erxleben)

Figures 72A, 74, 75

Voucher Material: AMNH 266566; MNHN 1998.678. Total = 2 specimens.

Identification: Members of the genus *Myoprocta*—commonly known as acouchies—are restricted to Amazonia, where most authors have recognized two species, one "red" (or "reddish") and the other "green" (or "greenish"), based primarily on coat-color differences. Despite this consensus, the diagnostic morphological characters and geographic distribution of red and green acouchies have yet to be convincingly documented by any published revisionary study based on museum specimens, and the nomenclature of *Myoprocta* species is currently confused.

Red and green acouchies can be distinguished unambiguously by a combination of external and cranial characters whose diagnostic value we tested by examining all of the *Myoprocta* specimens (including types) in five American and European museums (AMNH, BMNH, FMNH, MNHN, and USNM). In external appearance, most red acouchies are rich reddish-brown dorsally, with uniformly orange or reddish underparts, whereas most green acouchies are drab yellowish- or grayish-brown dorsally with yellowish underparts that are usually marked by white midventral streaks. Occasional skins of both the red and green species, however, have somewhat intermediate pigmentation. Thus, a few red acouchies (especially zoo specimens) have rather drab fur (e.g., AMNH 130148, BMNH 5.11.1.19, FMNH 21786), and a few green acouchies (e.g., AMNH 68243, BMNH 54.608) have warmer pelage tones than usual. Some coat-color variation is geographic in origin (e.g., red acouchies from the Guianas have generally less saturated pigments than Brazilian specimens from the north bank of the Amazon), but individual tonal differences also exist within most large series (e.g., 16 AMNH skins of green acouchies from San José Abajo, Ecuador). Nevertheless, the difference in coloration between red and green acouchies is conspicuous when typical exemplars of both kinds are viewed side-by-side.

Another obvious external difference is the presence in all red acouchies of a distinct rump patch of very long (60–80 mm) highly polished hairs that are typically much more heavily pigmented than the fur of the sides, middle back, and forequarters; in life, these hairs form a dark, glossy fringe that actually

extends beyond the rump to overlap the base of the tail (Emmons, 1990, 1997). Some specimens (e.g., AMNH 93043) have blackish rump hairs, but the usual color is a deep mahogany brown with or without inconspicuous basal bands of red. In a few Brazilian specimens (e.g., AMNH 94068, 94071; BMNH 20.7.1.23), the rump hairs are not substantially darker than the hairs of the sides and middle back, but they are still distinguishable from the fur of the latter parts by their length and high polish. By contrast, green acouchies never have a distinct rump patch, the fur over the hindquarters being essentially similar in length, color, and texture to the rest of the dorsal pelage.

Red acouchies are, on average, larger than green acouchies, a comparison that is best appreciated by craniometric comparisons of representative series (table 41). Visually, most red acouchy skulls have noticeably larger toothrows and bullae, broader interorbits, and longer nasals than most green acouchy skulls. Although no univariate measurement is diagnostic, red and green acouchies have nonoverlapping morphometric distributions in multivariate ordinations (e.g., by principal components analysis; not shown). Of the several qualitative cranial traits that Tate (1939: table IV) used to distinguish red and green acouchies, the most consistently useful is the size of the "palatal foramina" (= sphenopalatine vacuities), which perforate the bony roof of the mesopterygoid fossa; these are very narrow slits (<1 mm wide) in most specimens of red acouchies (fig. 72A), but they are wider (>1 mm) teardrop-shaped openings in most specimens of green acouchies (fig. 72B).

Based on specimens that we examined, red acouchies occur throughout Guyana, Surinam, French Guiana, and Brazil north of the Amazon and east of the Rio Branco (fig. 73). We are aware of only two vouchered records of red acouchies outside the Guiana subregion of Amazonia: (1) one specimen (AMNH 37123) collected by Leo E. Miller on 21 April 1914 on the "Lower Solimões", a locality that is now believed (see footnote 17) to correspond to Manacaparú, a settlement on the north bank of the upper Amazon just west of its confluence with the Rio Negro (locality 5 in fig. 73); and (2) two spec-

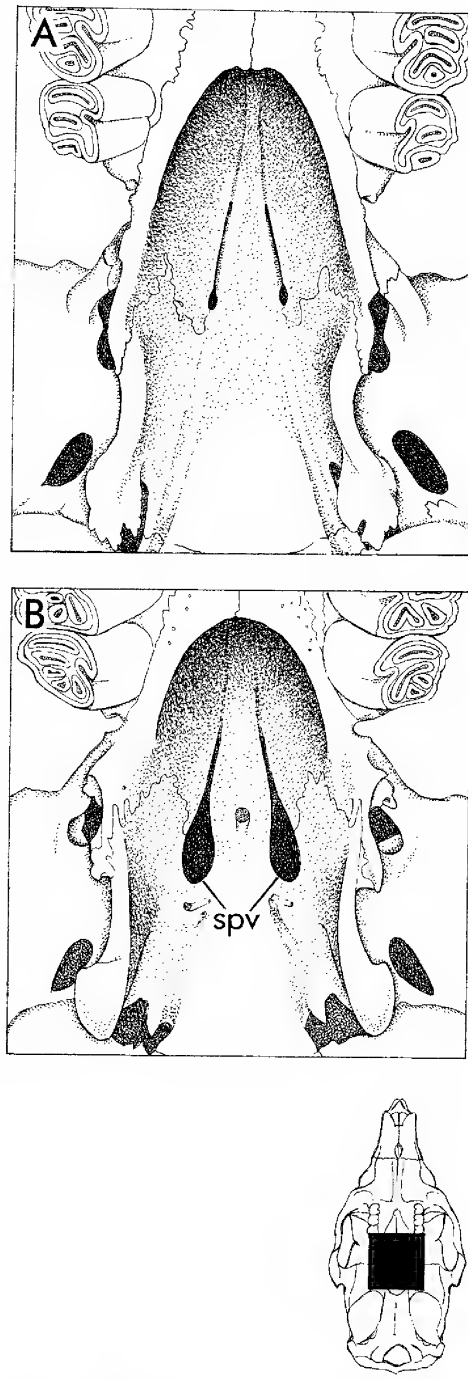

Fig. 72. Fenestration of the bony roof of the mesopterygoid fossa in typical examples of *Myoprocta acouchy* (**A,** AMNH 266566) and *M. pratti* (**B,** FMNH 125085). The sphenopalatine vacuities (**spv**) are usually present only as narrow (<1 mm) slits in the bony roof of the mesopterygoid fossa of *M. acouchy,* but in *M. pratti* these fenestrae are wider, teardrop-shaped apertures.

TABLE 41

Comparisons of Craniodental Measurements (mm) from Representative Samples of Adult Red Acouchies (*Myoprocta acouchy*) and Green Acouchies (*M. pratti*)

	Red acouchies[a]	Green acouchies[b]	*F*-value[c]
Sex	17 males, 8 females, 1 unk.	9 males, 11 females	
CIL	72.2 ± 2.7 (67.3–79.2) 26	67.8 ± 2.5 (63.7–71.6) 20	33.1**
LD[d]	21.7 ± 1.3 (19.0–25.4) 26	20.7 ± 1.3 (18.2–23.2) 20	6.3*
MTR[d]	13.8 ± 0.8 (12.4–15.5) 26	13.2 ± 0.5 (12.4–14.2) 20	9.4**
LN	27.3 ± 1.6 (25.0–31.8) 26	24.3 ± 1.3 (22.6–26.8) 20	45.5**
LIB	22.5 ± 1.0 (20.9–24.2) 26	20.0 ± 1.0 (18.4–22.0) 20	76.7**
ZL	22.7 ± 1.3 (19.9–24.5) 26	22.5 ± 0.8 (20.6–24.2) 19	0.4
ZB	38.6 ± 1.5 (35.6–40.8) 24	37.9 ± 1.6 (34.7–40.4) 19	2.0
BL[e]	16.1 ± 1.0 (14.5–18.5) 26	14.7 ± 0.6 (13.7–15.6) 15	21.9**

[a] The sample mean ± one standard deviation, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 93043, 94068, 94073, 94074, 94076, 94077, 266566; BMNH 3.4.6.6, 12.5.11.9, 12.6.5.28, 20.7.1.23, 27.8.11.52; FMNH 20019, 21785–21787, 93276, 93277, 95593, 95755, 95787; MNHN 1962.1329; USNM 338970, 339670, 546296, 546297.

[b] The sample mean ± one standard deviation, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 64007, 66775, 68226–68228, 68231–68233, 68236, 68237, 68242, 68243, 68247, 68249, 68250; FMNH 41485, 43189–43191, 125085.

[c] From 1-way ANOVAs: $*p < 0.05$, $**p < 0.01$.

[d] Alveolar measurements.

[e] Bullar length: the greatest antero-posterior dimension of one auditory bulla.

imens (FMNH 50895, 50896) collected by A. M. Olalla on 9 August 1936 at Lago do Baptista on the south bank of the Amazon between the Rio Madeira and the Rio Tapajos (locality 3 in fig. 73). Based on the latter record, we assume that unvouchered reports of unidentified *Myoprocta* from other sites along the south bank of the Amazon between the Madeira and the Tocantins (e.g., George et al., 1988; Voss and Emmons, 1996: appendix 8) were probably of red acouchies. Acouchies are apparently unknown east of the Rio Tocantins (Carvalho and Toccheton, 1969; Pine, 1973).

By contrast, green acouchies are extensively distributed in western Amazonia (west of the zoogeographic axis defined by the Rio Negro and the Rio Madeira), and they also occur in the headwaters of the Orinoco in southernmost Venezuela (Tate, 1939; Handley, 1976; Linares, 1998). Although a few published sources imply that red and green acouchies occur sympatrically in eastern Ecuador (Lönnberg, 1925) or eastern Colombia (Emmons, 1990, 1997), our specimen data suggest that red and green acouchies are allopatrically distributed. At least some of the historical uncertainty about the geographic ranges of red and green acouchies is due to the confused technical nomenclature for these animals.

Erxleben's (1777) original description of *Cavia acouchy* mentioned only small size, presence of a tail, and olivaceous coloration as characters distinguishing this species from other terrestrial hystricognaths then referred to the genus *Cavia*. Apparently, Erxleben did not examine any specimens himself, but instead based his description of *acouchy* on the earlier accounts of des Marchais (1730), Barrère (1741), Buffon (1767), and Pennant (1771) that he cited as references. We examined all of these early works and determined that Buffon and Pennant contain nothing more than rephrased versions of des Marchais' and Barrère's very brief reports about the "Agouchi" or "Akouchy" of Cayenne. By way of description, des Marchais stated only that the Agouchi is smaller and tastes better than the Agouti (*Dasyprocta leporina*), but Barrère (quoted verbatim by Tate [1935: 331] and Husson [1978: 471]) mentioned a tail and olive coloration.

There has never been any question that Erxleben's sources were describing a *Myoprocta* from French Guiana, but the refer-

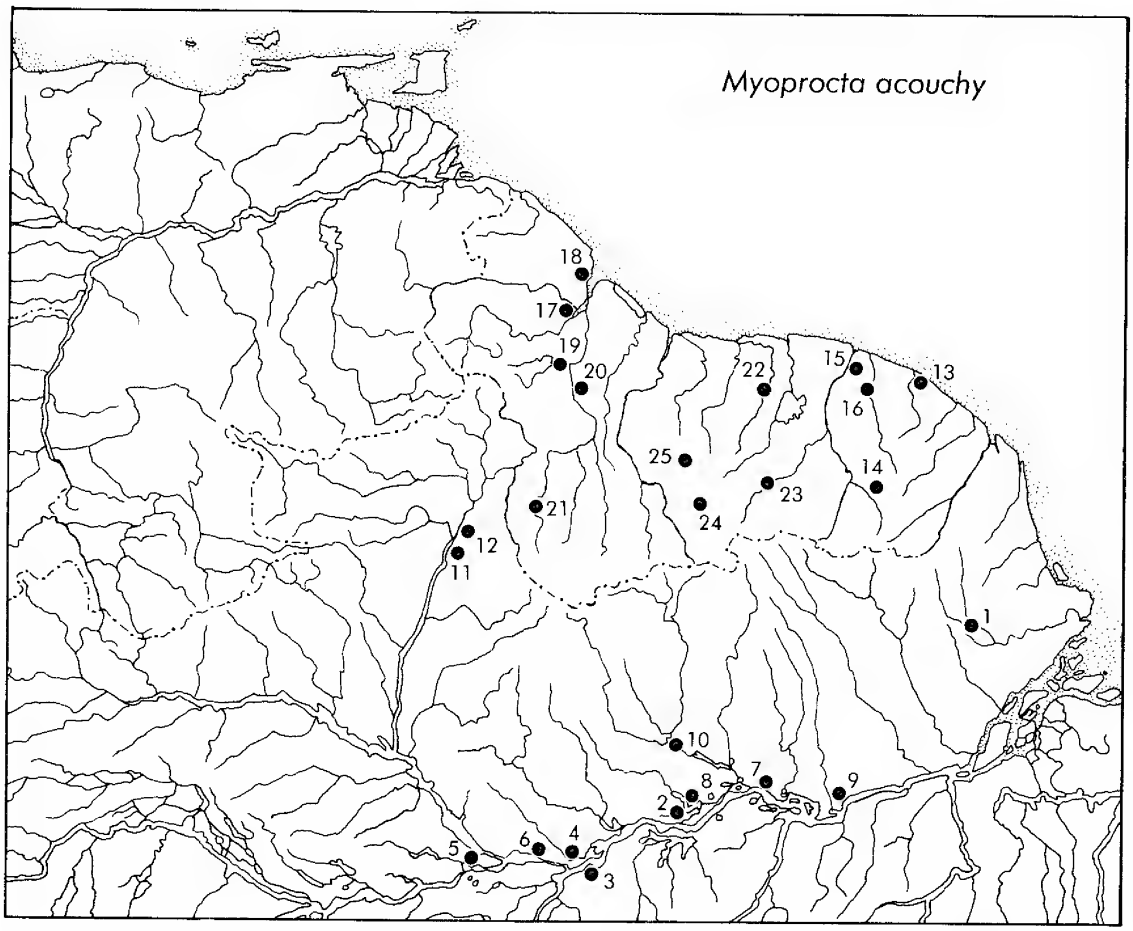

Fig. 73. Geographic range of *Myoprocta acouchy* based on specimens examined. **1,** BRAZIL, *Amapá,* Serra do Navio; **2,** BRAZIL, *Amazonas,* Boca Rio Piratucu; **3,** BRAZIL, *Amazonas,* Lago do Baptista; **4,** BRAZIL, *Amazonas,* Lago do Serpa; **5,** BRAZIL, *Amazonas,* Lower Solimões; **6,** BRAZIL, *Amazonas,* Santo Antonio do Amatari; **7,** BRAZIL, *Pará,* Colonia do Veado; **8,** BRAZIL, *Pará,* Faro; **9,** BRAZIL, *Pará,* Monte Alegre; **10,** *Pará,* Cachoeira Porteira; **11,** *Roraima,* Conceição; **12,** BRAZIL, *Roraima,* Serra Grande; **13,** FRENCH GUIANA, Paracou; **14,** FRENCH GUIANA, Saut Macaque; **15,** FRENCH GUIANA, St.-Laurent du Maroni; **16,** FRENCH GUIANA, Tamanoir; **17,** GUYANA, *Cuyuni-Mazaruni,* Kartabo; **18,** GUYANA, *Pomeroon-Supenaam,* Supinaam River; **19,** GUYANA, *Potaro-Siparuni,* Potaro; **20,** GUYANA, *Upper Demerara-Berbice,* Moraballi; **21,** GUYANA, *Upper Takutu-Upper Essequibo,* Dadanawa; **22,** SURINAM, *Brokopondo,* Locksie Hattie; **23,** SURINAM, *Marowijne,* Paloemeu Camp; **24,** SURINAM, *Nickerie,* Kaiserberg Airstrip; **25,** SURINAM, *Nickerie,* Wilhelmina Mountains.

ence to olive coloration has led to conflicting taxonomic applications of the epithet *acouchy.* Thomas (1926: 639) argued that this name applies to the reddish species based on the geographic origin of des Marchais' and Barrère's observations, noting that "many specimens of this animal are of a somewhat olivaceous tone, which, in the absence of [*M.*] *pratti* [the green acouchy], might easily justify the word being applied to them." Cabrera (1961) agreed, noting that Erxleben's original sources were not professional naturalists and might have been describing the species inaccurately from memory. By contrast, Tate (1939), Carvalho (1962), and Husson (1978) applied the name *acouchy* to the green species based on Barrère's color description; according to these authors, the red

acouchy should be called *M. exilis* (Wagler, 1831).

The crux of this disagreement is whether geography or color is to be given greater importance in applying the name *acouchy*. In the absence of an extant type,[20] the issue cannot be definitely resolved, and both of the conflicting usages mentioned above are current in the literature (e.g., Woods, 1993; Emmons, 1990, 1997). Since the geographic datum is definite whereas the color description is subject to interpretation, we favor Thomas's (1926) and Cabrera's (1961) usage, which also avoids the absurdity of making French Guiana—where only red acouchies are known to occur—the type locality for the green species. In order to fix this application of *Myoprocta acouchy* and thereby stabilize the species-level nomenclature of *Myoprocta,* we select as the neotype of *Cavia acouchy* Erxleben (1777) our adult Paracou voucher, AMNH 266566, consisting of a well-preserved skin (fig. 74), skull (fig. 75), and postcranial skeleton; measurements of this specimen are provided in table 42 along with those of other conspecific adults from French Guiana.

Our assignment of nominal taxa in the genus *Myoprocta* to either the red or green species groups (table 43) is based on first-hand examination of types and/or original descriptions. Although some Brazilian specimens of red acouchies are larger and redder than most specimens from Guyana, Surinam, or French Guiana, all red acouchies closely resemble one another and we see no compelling evidence that more than a single species is represented. Green acouchies, however, appear to exhibit significant geographic variation and may eventually prove to be a complex of closely related species; nevertheless, all can be provisionally referred to *M. pratti* pending a comprehensive study of this group.

Other Specimens Examined: **Brazil**—*Amapá,* Serra do Navio (USNM 546313); *Amazonas,* Boca Rio Paratucu on Rio Jamundá (AMNH 94073–94075), Lago do Baptista on Rio Amazonas (FMNH 50895, 50896), Lago do Serpa on Rio Amazonas (FMNH 50897), "Lago do Taraci on Rio Negro" (BMNH 27.8.11.52), Lower Solimões (AMNH 37123), Santo Antonio do Amatari (AMNH AMNH 92886–92888, 93043); *Pará,* "Castanhal on Rio Jamundá" (AMNH 94076), Colonia do Veado (BMNH 12.5.11.9), Faro (AMNH 94068–94072), Monte Alegre (BMNH 20.7.1.23), Cachoeira Porteira (USNM 546296, 546297), San José on Rio Jamundá (AMNH 94077); *Roraima,* Conceição (FMNH 20007), Serra Grande (FMNH 20019). **French Guiana**—Saut Macaque (MNHN 1962.1329), St.-Laurent du Maroni (MNHN 1909.243), Tamanoir on Mana River (FMNH 21783, 21785–21787), no other locality data (MNHN 1962.1330, 1974.268). **Guyana**—"Bonasica on Essequibo River" (AMNH 36493 [type of *demerarae*], BMNH 12.6.5.28, 13.5.23.6–13.5.23.9), "Kuitaro River" (USNM 338969–338971), "Manarica Creek on Essequibo River" (BMNH 13.6.8.11), "Moon Mountains" (BMNH 11.6.7.45), "Supinaam River" (BMNH 20.7.1.20–20.7.1.22); *Cuyuni-Mazaruni,* Kartabo (AMNH 8178); *Potaro-Siparuni,* Potaro (BMNH 3.4.6.6, 3.4.6.7); *Upper Demerara-Berbice,* "Comackka on Demerara River" (BMNH 5.11.1.19), Moraballi (BMNH 34.6.30.57–34.6.30.61); *Upper Takutu-Upper Essequibo,* Dadanawa (USNM 339670). **Surinam**—*Brokopondo,* Locksie Hattie (FMNH 95753 [two specimens with this number]); *Marowijne,* Paloemeu Camp on Tapahoni River (FMNH 95593, 95754, 95787); *Nickerie,* Kaiserberg Airstrip on Zuid River (FMNH 93270–93277), Wilhelmina Mountains on West River (FMNH 95755).

Field Observations: We frequently heard the alarm calls of *Myoprocta acouchy* and we caught glimpses of fleeing individuals on many occasions, but we seldom obtained an unobstructed view of the animal in repose. Our single adult voucher was taken on the

[20] According to Husson (1978: 472), "we may consider Barrère's specimen to be the lectotype of this species", but it is unclear whether Barrère actually saw an acouchy himself or was merely repeating what he had been told about it by natives. Geoffroy (1803: 167) mentioned an old Paris museum specimen ("Individu provenant de l'ancien cabinet") of *Cavia acuschi* [sic] that might have been seen by Barrère, but Rode (1945) did not list it in his catalog of MNHN rodent types, and the museum does not now contain any 18th-century specimens of *Myoprocta* (L. Granjon, personal commun.). In the absence of any indication to the contrary, we assume that the lectotype no longer exists.

Fig. 74. Dorsal and ventral views of the skin of AMNH 266566, neotype of *Cavia acouchy* Erxleben, 1777 (= *Myoprocta acouchy*). Both views about ×0.3.

Fig. 75. Dorsal, ventral, and left lateral views of the skull of AMNH 266566, neotype of *Cavia acouchy* Erxleben, 1777 (= *Myoprocta acouchy*). All views approximately ×1.3.

TABLE 42
Measurements (mm) and Weight (kg) of the Neotype and Other Specimens of *Myoprocta acouchy* from French Guiana

		Other specimens			
	Neotype[a]	MNHN 1962.1329	FMNH 21786	FMNH 21785	FMNH 21787
Sex	male	male	male	female	female
HBL	360	—	343	346	300
LT	67	—	51	59	59
HF	93	—	89	91	94
Ear	35	—	—	—	27
CIL	71.1	73.1	67.6	70.4	69.3
LD[b]	21.9	22.1	19.0	20.4	20.9
MTR[b]	13.3	14.2	13.9	14.5	12.6
LN	25.3	28.6	25.3	27.4	27.2
LIB	22.8	23.9	21.2	24.0	23.2
ZL	20.6	24.0	19.9	21.7	21.9
ZB	36.7	39.1	35.6	38.2	38.1
BL[c]	15.4	15.8	14.5	15.3	14.9
Wt	1.2	—	—	—	—

[a] AMNH 266566, from Paracou (see text).
[b] Alveolar measurements.
[c] Bullar length: greatest antero-posterior measurement of one auditory bulla.

ground in a leghold trap in swampy primary forest, and a juvenile specimen was subsequently taken in a Victor trap tied to the base of a broad liana 50 cm above the ground in well-drained primary forest. Four unvouchered observations recorded in our fieldnotes document the presence of this species in well-drained primary forest, swampy primary forest, creekside primary forest, and secondary vegetation. Most of our sightings were diurnal, usually in the very early morning or late afternoon, but a few animals were flushed from their hiding places at night.

CUNICULIDAE

Only a single cuniculid species occurs at Paracou. The lowland paca is unmistakable in external and craniodental characters and cannot be confused with any other species of Guianan mammal.

Cuniculus paca (Linnaeus)

VOUCHER MATERIAL: AMNH 265954, 266567, 266569; MNHN 1998.679. Total = 4 specimens.

TABLE 43
Species Groups, Nominal Taxa, and Type Localities of Acouchies (Genus *Myoprocta*)

	Type locality
Red acouchy group	
acouchy Erxleben (1777)	Paracou, French Guiana[a]
exilis Wagler (1831)[b]	Amazon River, Brazil[c]
leptura Wagner (1844)	Rio Negro, Brazil[d]
demararae Tate (1939)	Bonasica, Essequibo River, Guyana
Green acouchy group	
pratti Pocock (1913)	Pongo de Rentema, Río Marañón, Peru[e]
milleri Allen (1913a)	La Murelia, Caquetá, Colombia
limanus Thomas (1920)	Acajutuba, Rio Negro, Brazil
parva Lönnberg (1921)[f]	Río Curaray, Ecuador
archidonae Lönnberg (1925)	Archidona, Ecuador
caymanum Thomas (1926)	Canabouca, Paraná do Jacaré, Brazil
puralis Thomas (1926)	Ayapua, Brazil

[a] Fixed by neotype selection in this report.
[b] Considered to be a green acouchy by Allen (1916b), but a red acouchy by Thomas (1917) and most subsequent authors. Possibly, Allen's identification was based on Wagler's reference to a white midventral line, a common trait in green acouchies, but occasional specimens of red acouchies (e.g., AMNH 92886) also show white midventral markings. If the type is not extant, any future use of this name for a valid taxon of *Myoprocta* should be fixed by designating a neotype. This would be an appropriate name for the slightly larger and more richly pigmented red acouchy of Brazil, if this were to prove distinct from the typical form in Guyana, Surinam, and French Guiana.
[c] "Habitat in Brasilia ad flumen Amazonum" (Wagler, 1831: 622). Allen (1916b: 569) said that the type was collected by Spix "presumably near the mouth of the Rio Negro" but he did not explain the basis for this inference.
[d] Wagner's type series was collected by Natterer, possibly at "Barra do Rio Negro" (= Manaus), the only definite locality where Natterer is known to have taken acouchies (Pelzeln, 1883).
[e] See Thomas (1920: 279, footnote).
[f] Said to be a red acouchy by Lönnberg (1925) and Tate (1939), but the original description of *parva* is impossible to reconcile with that identification. Instead, every detail of Lönnberg's (1921) text indicates that the specimens in hand were green acouchies.

IDENTIFICATION: Our specimens are topotypes of this species (the type locality of which was restricted to French Guiana by Tate, 1935) and agree closely with Husson's

(1978) detailed description and illustrations of Surinamese material. Selected measurements (mm) and weights (kg) of two adult male vouchers (AMNH 265954, MNHN 1998.679) are: HBL 650, 739; LT 0, 11; HF 115, 121; Ear 52, 53; CIL 138.1, 134.4; LD 54.3, 52.7; MTR 27.3, 30.5; LN 52.4, 51.0; LIB 41.2, 42.4; ZL 72.3, 77.0; ZB 98.4, 105.2; Wt 9.5, 9.2.

The lowland paca ranges from southern Mexico to Paraguay, and several subspecies have been recognized as valid by authors (e.g., Krumbiegel, 1940b; Cabrera, 1961). Although Krumbiegel (1940b) cited pelage and cranial characters to justify his trinomial distinctions, no comprehensive review of geographic variation in this species based on the very large museum collections now available for study has yet been attempted. In the absence of such a critical undertaking, a subspecific nomenclature does not seem warranted at present; however, our material would obviously represent the nominate race if trinomials were to be recognized in any future revision.

In a recently published opinion, the International Commission on Zoological Nomenclature (ICZN, 1998) ruled that *Cuniculus* was available from Brisson (1762), thus replacing *Agouti* Lacépède (1799) as the oldest valid generic name for the lowland paca.

Field Observations: We collected four specimens of *Cuniculus paca* at Paracou and recorded 24 unvouchered observations in our fieldnotes. Habitat information accompanying 26 records include 7 encounters (27%) in well-drained primary forest, 4 (15%) in swampy primary forest, 6 (23%) in creekside primary forest, 1 (4%) in primary forest of unspecified character, and 9 (35%) in secondary vegetation; all encounters were nocturnal. Pacas were encountered singly, except in rare cases when we witnessed agonistic encounters between two adults or saw an adult female accompanied by a juvenile. Most individuals were sighted on the ground, but one individual was submerged in a stream under a fallen tree, apparently attempting to hide underwater.

Echimyidae

We captured or observed four echimyid species at Paracou, including representatives of the genera *Makalata, Mesomys,* and *Proechimys.* Based on collections from other localities in French Guiana and Surinam (appendix 1), it seems probable that two additional echimyids could occur locally. Although species of *Proechimys* can only be distinguished from one another with adult specimens in the hand, other French Guianan echimyids can be identified at a distance by well-marked external characters (Emmons, 1990, 1997) if a sufficiently clear view is obtained. Unfortunately, although the taxa in question are readily distinguished, their nomenclature is still problematic in some cases.

Makalata didelphoides (Desmarest)

Our only record of this species at Paracou is an unambiguous sighting by DPL of a solitary adult perched on a tree trunk 3 m above a small stream in primary forest at 10:30 hours on 27 October 1992.

In most of the older literature (e.g., Tate, 1935, 1939; Cabrera, 1961) this species is called *Echimys armatus* (I. Geoffroy), but Husson (1978) proposed the new genus *Makalata* with *armatus* as type species in recognition of the well-marked craniodental differences between this taxon and *Echimys chrysurus* (the type species of *Echimys* G. Cuvier). For the use of *didelphoides* to replace *armatus* as the oldest available name for the red-nosed tree rats of the Guiana subregion of Amazonia, see Emmons (1993b).

Mesomys sp.

Voucher Material: AMNH 266596.

Identification: The genus *Mesomys* has never been revised and the identification of its constituent species has long been problematic. Woods (1993) recognized *M. didelphoides* (Desmarest), *M. hispidus* (Desmarest), *M. leniceps* Thomas, *M. obscurus* (Wagner), and *M. stimulax* Thomas as valid species, but Emmons (1993b) showed that *didelphoides* and *obscurus* both belong in the genus *Makalata,* and Patton et al. (2000) subsequently described a new species, *Mesomys occultus.* Therefore, current usage would now recognize four valid species of *Mesomys*: *M. hispidus* (including *ecaudatus* Wagner, *ferrugineus* Günther, and *spicatus* Thomas as synonyms; after Woods, 1993), *M. leniceps, M. occultus,* and *M. stimulax.*

In order to identify our single Paracou voucher, we consulted the original descriptions of all nominal taxa currently referred to *Mesomys,* and we examined the holotypes of every named form except *ecaudatus.* In addition, we measured relevant series of specimens in the AMNH, USNM, and BMNH to assess geographic variation in morphometric characters. Below we explain why, despite this effort, we are still unable to confidently assign a specific epithet to our material.

Of all the material we examined, the most distinctive is the holotype of *Mesomys leniceps* from the Andean highlands of eastern Peru. This specimen (BMNH 26.8.6.61) is distinguished from all other congeners by its much longer tail (relative to head-and-body length), finer and denser tail hairs, finer and softer spines, more convergent toothrows, posteriorly constricted incisive foramina, and much smaller bullae. By contrast, Amazonian specimens of *Mesomys* (including all of the remaining nominal taxa in this genus) have relatively shorter tails, coarser spines and tail hairs, less convergent toothrows, posteriorly unconstricted incisive foramina, and larger bullae. Although we searched diligently for external and craniodental character variation among Amazonian samples of *Mesomys,* only maxillary toothrow length appears to offer any broadly useful morphological basis for taxonomic inference.

The first example of *Mesomys* to be reported from any of the Guianas was a Surinamese specimen that Husson (1978) identified as *M. stimulax.* We have examined five additional specimens (table 44) from the Guiana subregion, including our Paracou voucher, all of which essentially resemble Husson's material and appear to represent the same taxon despite substantial variation in some cranial dimensions (plausibly attributable to age differences) and in external proportions (perhaps attributable to measurement artifacts). Consistent with Husson's identification, these Guianan specimens have small toothrows (MTR = 5.9–6.6 mm) that fall within the range of variation exhibited by specimens referable to *stimulax* from southeastern Amazonia (right-hand column, table 44). By contrast with these small-toothed Guiana and Southeastern subregion samples, all western Amazonian *Mesomys* samples have mean toothrow lengths greater than 7 mm (e.g., the series measured by Patton et al., 2000: tables 56, 58). Small-toothed and large-toothed *Mesomys* are sympatric at Igarapé Amorim on the left (west) bank of the Rio Tapajos (specimens in AMNH), but elsewhere these morphometric classes appear to be allopatric. Although it is geographically part of the Guiana subregion of Amazonia, the Venezuelan state of Amazonas is inhabited by large-toothed *Mesomys* (e.g., nine USNM specimens with a mean maxillary toothrow length of 7.2 mm), an observation consistent with the presence of other western Amazonian taxa (e.g., *Dasyprocta fuliginosa, Myoprocta pratti*; see above) in that area.

Although western Amazonian *Mesomys* specimens have often been identified as *M. hispidus* (e.g., by Cabrera, 1961; da Silva and Patton, 1993; Patton et al., 1994, 2000; Voss and Emmons, 1996), this usage appears to be incorrect. The maxillary toothrow of the type of *hispidus*[21] measures 6.4 mm, well outside the observed range of variation in this dimension for any known western Amazonian sample. Unfortunately, it is not known exactly where the type was collected. Desmarest (1817) gave the type locality as "l'Amérique méridionale", but the specimen was almost certainly obtained by Alexandre Rodriguez Ferreira,[22] whose known collect-

[21] Rode's (1945) catalog of MNHN rodent types lists that of *Echimys hispidus* as a mounted specimen (number 1806 in the old "montage" series of the MNHN) from which the skull had been extracted and lost. The skull, however, identified as that of the type by a BMNH label in Thomas's handwriting, is still preserved as A-7668 in the nearby Laboratoire d'Anatomie Comparée. Emmons (1993b) and RSV independently examined both skin and skull, which we judge to be correctly associated in the absence of any indication to the contrary.

[22] The 19th-century wooden base on which the type skin of *Mesomys hispidus* is still mounted bears the inscription "du Cabinet de Lisbonne 1808", indicating that this specimen was part of the plunder that Napoleon's troops shipped to Paris following the sack of Lisbon. That shipment apparently included the entire collection of natural history specimens assembled in Brazil between 1783 and 1792 by Ferreira, an employee of the Museu Royal d'Ajuda (Hershkovitz, 1987a). Significantly, the primates illustrated in Ferreira's "Viagem Filosófica" include two taxa (*Chiropotes satanas chiropotes* and *Saguinus midas midas*; op. cit.: table 2) that must have been collected or observed in the Guiana subregion of Amazonia, where the type of *Mesomys hispidus* might also have been taken.

TABLE 44

Measurements (mm) and Weights (g) of Adult Specimens of Small-Toothed *Mesomys* from the Guiana and Southeastern Subregions of Amazonia

	Guiana subregion					Southeastern subregion	
	LHE 968[a]	RMNH 21728[b]	AMNH 266596[c]	V-924[d]	USNM 543283[e]	BMNH 11.4.28.29[f]	Other specimens[g]
Sex	female	female	male	male	male	female	8 males, 7 females
HBL	150	129	140	149	180	158	169 ± 13 (154–196) 11
LT	—	113	141	157	—	122	154 (122–199) 7
HF	30	28	28	28	29	31	30 ± 2 (28–33) 12
Ear	14	11	15	12	13	13	13 (12–13) 3
CIL	36.6	34.8	31.3	33.4	37.2	36.1	37.3 ± 2.1 (33.9–40.1) 13
LD	8.8	8.7	7.3	7.8	8.7	8.7	9.0 ± 0.6 (8.2–10.0) 14
MTR	6.6	6.3	5.9	6.2	6.4	6.6	6.3 ± 0.3 (5.8–6.8) 14
BM1	1.8	1.9	1.6	1.7	1.8	2.0	1.8 ± 0.1 (1.6–2.0) 13
LIF	3.4	3.6	3.0	3.0	3.6	3.1	3.4 (2.9–3.8) 8
BIF	1.3	1.3	1.5	1.6	1.4	1.4	1.4 (1.2–1.7) 9
LN	11.6	10.7	10.5	10.0	12.1	11.2	11.8 ± 0.9 (10.4–13.1) 14
LIB	10.4	9.0	8.4	9.5	10.1	11.1	10.4 ± 0.6 (9.4–11.5) 13
ZL	14.5	13.6	12.9	13.5	15.7	14.4	14.9 ± 0.6 (14.0–16.1) 13
ZB	21.6	21.1	20.1	21.0	21.8	21.3	21.5 ± 0.9 (20.0–23.1) 14
Wt	139	—	78	98	132	—	—

[a] From Maipaima Creek in the West Kanuku Mountains, Upper Takutu–Upper Essequibo, Guyana; eventually to be cataloged in the UG. Cytochrome-b sequence data from this specimen were analyzed by Patton et al. (2000).

[b] From the Vier Gebroeders Mountains, near Sipaliwini, Nickerie District, Surinam. Measurements from Husson (1978) and courtesy of C. Smeenk.

[c] Paracou voucher.

[d] From Arataye, French Guiana; eventually to be cataloged in the MNHN. Ethanol-preserved tissues from this specimen are cataloged as T-1916 in the research collection of F. Catzeflis at the Institut des Sciences de l'Évolution, Université Montpellier 2, Montpellier, France.

[e] From Serra do Navio, Amapá, Brazil.

[f] Holotype of *Mesomys stimulax*; from Cametá, on left (west) bank of the lower Rio Tocantins, Pará, Brazil.

[g] From the left (west) bank of the lower Rio Tapajos eastward to Marajó Island. The mean ± one standard deviation, the observed range (in parentheses), and the sample size are provided for measurements of the following specimens: AMNH 95538, 95541–95544, 95546, 95971, 96773; BMNH 5.1.25.5, 20.7.1.25, 24.2.4.15; USNM 521541, 544641, 549592.

ing itinerary (reproduced by Hershkovitz, 1987a: fig. 3) was largely confined to Amazonian Brazil. Tate (1935) proposed restricting the type locality of *hispidus* to Borba, a settlement on the right bank of the lower Rio Madeira where Natterer collected the type of *ecaudatus* in 1830 (Pelzeln, 1883). Tate's action was biologically arbitrary but served to justify his synonymization of *hispidus* and *ecaudatus,* the types of which he had not seen. Unfortunately, two species of *Mesomys* with divergent toothrow measurements are known to occur in the interfluvial region between the Madeira and the Tapajos (e.g., at Igarapé Amorim, see above) and it is not known whether the type of *ecaudatus* is a small-toothed animal (like *hispidus*) or not. Until the type of *ecaudatus* is examined and measured, the oldest available name based on a large-toothed *Mesomys* specimen is *ferrugineus* Günther (1876) from northeastern Peru.

Based simply on toothrow measurements, our Paracou voucher and other similar specimens from the Guiana subregion of Amazonia could justifiably be referred to *Mesomys hispidus,* of which *stimulax* is perhaps only a junior synonym. However, Patton et al. (2000) reported high cytochrome-b sequence divergence between small-toothed *Mesomys* specimens from opposite sides of the Amazon, a result that clearly indicates the

insufficiency of toothrow length as a basis for taxonomic inference and brings into sharper focus the problem of exactly where the type of *hispidus* was collected (see footnote 22). For the moment, these are insoluble problems for which the only appropriate interim solution is to leave our voucher material unnamed.

Other Small-Toothed Specimens Examined from the Guiana Subregion: **Brazil**—*Amapá,* Serra do Navio (USNM 543283). **French Guiana**—Les Nouragues (V-924). **Guyana**— *Potaro-Siparuni,* 5 km SE Surama (ROM 103346); *Upper Takutu-Upper Essequibo,* Maipaima Creek in Kanuku Mountains (LHE 968, an uncataloged specimen to be deposited in UG).

Field Observations: Our single record of *Mesomys* from Paracou is based on a specimen taken in a Victor trap tied to a broad liana 1.9 m above the ground in swampy primary forest.

Proechimys J. A. Allen

The last comprehensive revision of the genus *Proechimys* was Moojen's (1948) monograph, but subsequent research has resulted in substantial modifications of his pioneering taxonomic synthesis. In particular, studies of well-sampled local faunas have proven crucial for distinguishing patterns of morphological, karyotypic, and molecular variation within and among sympatric species of *Proechimys,* especially in western Amazonia where four or more occur at some localities (Patton and Gardner, 1972; da Silva, 1998; Patton et al., 2000). To date, however, no equivalent studies of character variation within and among sympatric *Proechimys* species from other Amazonian subregions have been published.

Until quite recently, only a single widespread species of *Proechimys,* variously identified as *P. guyannensis* (E. Geoffroy, 1803) or as *P. cayennensis* (Desmarest, 1817), was recognized in the Guianas (e.g., by Tate, 1935; Cabrera, 1961). In 1978, however, A. M. Husson (at the Rijksmuseum van Natuurlijke Historie, Leiden) and F. Petter (at the Muséum National d'Histoire Naturelle, Paris) independently reported the occurrence of two sympatric forms in Surinam and in French Guiana, respectively. Although both authors recognized a common large species and a rarer small species, they gave different accounts of diagnostic nonmetrical characters and they used different nomenclature.

Husson (1978) identified his large Surinamese specimens as *Proechimys guyannensis* (E. Geoffroy, 1803), and his small specimens as *P. warreni* Thomas (1905). In Husson's opinion, measurements of the cheekteeth provided the best diagnostic criterion: 18 specimens of the large Surinamese species had maxillary toothrow lengths of 8.3–9.2 mm, whereas 6 specimens of the small species had cheektooth measurements of 7.2–7.7 mm. Husson also reported that his large species was more abundant, and had more rufous pelage, a relatively shorter tail, less appressed caudal hairs, and a wider mesopterygoid notch in the back of the hard palate than his small species (op. cit.: 429–438). Husson based his identification of the large species primarily on Geoffroy's (1803) description of pelage color in *guyannensis* because the skull of the type (not measured by Geoffroy) was thought to have been lost (Rode, 1945). Husson's identification of the small species, however, was based on direct external and craniodental comparisons with the type of *warreni.*

Petter (1978) reported the rediscovery of the type skull of *Proechimys guyannensis* and assigned this name to the smaller (and rarer) of the two forms found in French Guiana; the larger (and more abundant) form, apparently undescribed, was then named as a new species, *P. cuvieri.* However, whereas Husson found that the large and small Surinamese species were nonoverlapping in maxillary toothrow length, Petter reported overlapping variation in this measurement, with observed ranges of 7.0–8.5 mm for *guyannensis* and 8.1–9.3 mm for *cuvieri.* Petter did not mention the other distinguishing characters discussed by Husson, but he noted karyotypic differences (2N = 40 in *guyannensis,* 2N = 28 in *cuvieri*) and differences in the number of enamel islands of the lower cheekteeth (two per tooth in *guyannensis,* three in *cuvieri*). The karyotypes of *guyannensis* and *cuvieri* were subsequently described in greater detail by Reig et al. (1979).

In an important review of morphological

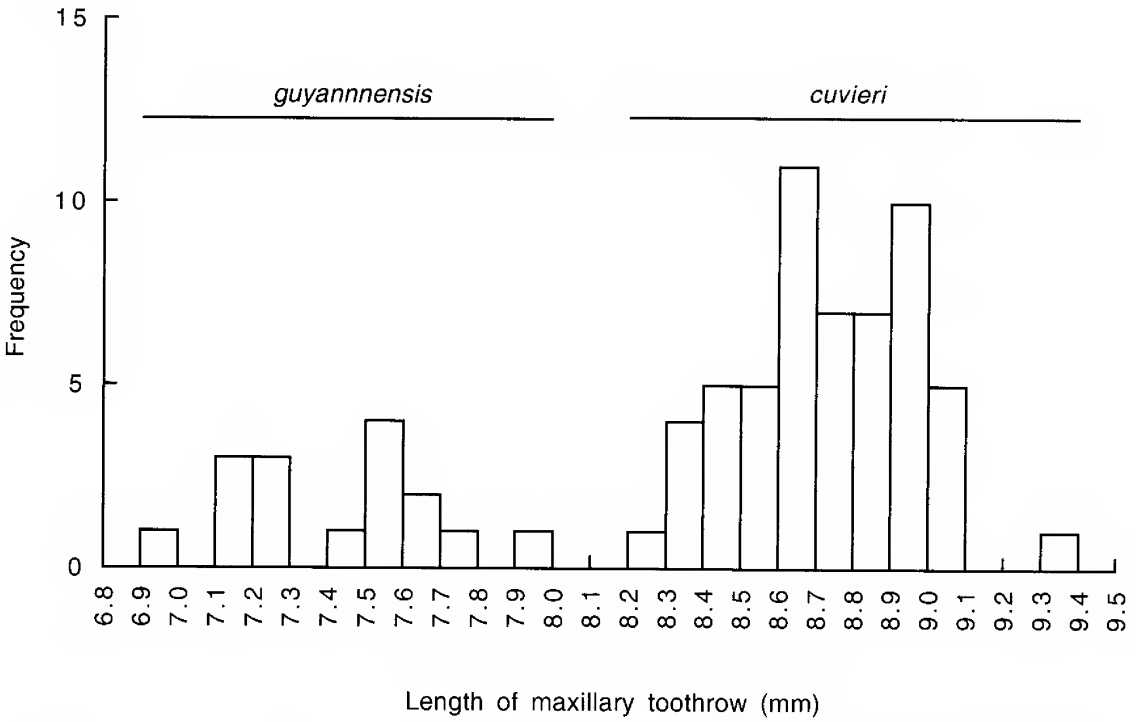

Fig. 76. Frequency histogram of maxillary toothrow length (MTR) for all measured French Guianan specimens of *Proechimys* (N = 72; see text).

variation in *Proechimys,* Patton (1987) identified several qualitative characters distinguishing clusters of populations assigned to his *cuvieri* and *guyannensis* species groups. However, Patton's study included no French Guianan material, so the diagnostic value of the characters he investigated is unknown for the local populations sampled by our study. Indeed, Guillotin and Ponge (1984: 287) doubted that *cuvieri* and *guyannensis* could be distinguished by "méthodes morphologiques classiques", a conclusion based on bivariate and multivariate analyses that showed no obvious morphometric discontinuity among French Guianan specimens representing both of the karyomorphs reported by Petter (1978) and Reig et al. (1979). The apparent lack of diagnostic external characters between *guyannensis* and *cuvieri* has also been an impediment for ecologists unable to identify these species by nondestructive sampling in field studies (e.g., Forget, 1991).

The morphological characters of French Guianan populations of *Proechimys cuvieri* and *P. guyannensis* are important because both species are based on types collected in French Guiana (Petter, 1978). Additionally, the application of these names to the sympatric Surinamese forms reported by Husson remains to be evaluated. In order to identify our Paracou vouchers, and to provide a basis for future revisionary research with these species, we examined most of the *Proechimys* specimens from French Guiana currently held in American and European museums. Except as noted below, our results are based on measurements and qualitative character data obtained from fully adult but nonsenescent animals, herein defined as members of age categories 8 and 9 of Patton and Rogers (1983). The following results of our analyses broadly overlap those independently obtained by Catzeflis and Steiner (2000), who examined many of the same specimens.

Maxillary toothrow measurements of nonsenescent adult *Proechimys* from French Guiana form two distributions (fig. 76): a sparse cluster of small specimens with cheekteeth measuring 6.9–8.0 mm, and a denser cluster of larger specimens with longer tooth-

TABLE 45
Measurements (mm) and Weights (g) of Adult *Proechimys cuvieri* and *P. guyannensis* from French Guiana[a]

		guyannensis	
	cuvieri[b]	Type[c]	Other specimens[d]
Sex	27 males, 29 females	unknown	7 males, 9 females
HBL	234 ± 19 (190–287) 52	—	189 ± 16 (156–209) 14
LT	168 ± 13 (142–196) 40	—	145 ± 20 (110–186) 13
HF	51 ± 2 (45–56) 55	42	44 ± 2 (41–49) 15
Ear	24 ± 2 (18–27) 53	—	22 ± 2 (18–26) 15
CIL	47.1 ± 2.6 (40.3–52.4) 51	—	39.7 ± 1.9 (37.3–43.4) 15
LD	12.3 ± 0.7 (10.9–14.3) 55	11.5	10.0 ± 0.6 (9.5–11.2) 16
MTR	8.7 ± 0.2 (8.2–9.3) 56	7.3	7.4 ± 0.3 (7.0–8.0) 16
LIF	5.7 ± 0.5 (4.6–6.7) 55	5.0	4.7 ± 0.6 (3.8–5.9) 16
BIF	3.0 ± 0.3 (2.4–4.2) 55	2.2	2.5 ± 0.2 (2.1–2.8) 16
LN	21.7 ± 1.7 (18.7–26.3) 55	—	18.2 ± 1.3 (16.8–21.3) 13
LIB	12.6 ± 0.8 (10.8–14.1) 53	10.0	10.4 ± 0.5 (9.6–11.2) 16
ZL	18.4 ± 1.0 (15.8–20.4) 54	15.8	15.7 ± 0.7 (14.8–17.3) 16
ZB	26.9 ± 1.3 (23.7–29.9) 53	22.8	23.1 ± 0.9 (21.2–24.4) 15
Wt	343 ± 96 (166–645) 30	—	191 ± 47 (136–271) 9

[a] Except as noted, all measured specimens are assignable to age categories 8 and 9 of Patton and Rogers (1983). For both species, summary statistics include the sample mean ± one standard deviation, the observed range (in parentheses), and the sample size.

[b] AMNH 266570, 266572–266574, 266589, 266591, 266592, 266594, 267025, 267027–267029, 267039, 267041, 267602; MNHN 1970.223, 1972.639, 1974.263, 1974.266, 1977.774 (holotype), 1981.23, 1981.24, 1981.26, 1981.29–1981.33, 1981.36, 1981.46, 1981.50, 1981.54, 1981.56, 1981.107, 1982.523, 1983.378, 1986.1129, 1995.3220–1995.3222, 1995.3224, 1998.314, 1998.315, 1998.685, 1998.688, 1998.689, 1998.691, 1998.692, 1998.695–1998.698, 1998.1821; USNM 548450–548452.

[c] MNHN 1995.1395, an old adult (age class 10 of Patton and Rogers, 1983).

[d] AMNH 266595, 267037, 267047; MNHN 1981.48, 1982.601, 1983.374–1983.376, 1983.381, 1986.1130, 1994.128, 1998.312, 1998.683; USNM 548454–548456.

rows (8.2–9.3 mm). Following Petter (1978), we associate the name *guyannensis* with the smaller-toothed form based on the toothrow dimensions of the holotype (MNHN 1995.1395, an old adult), which has an alveolar measurement of 7.8 mm and an estimated crown measurement of 7.3 mm (table 45). The larger-toothed specimens that we measured include the type of *cuvieri,* MNHN 1977.774, which has a crown-length toothrow measurement of 8.5 mm. To supplement this essentially univariate distinction, we examined qualitative variation in craniodental, external, and genitalic characters to determine whether or not *Proechimys* with small versus large cheekteeth differ in other respects.

We scored the septum that separates the right and left incisive foramina as "complete" or "incomplete" (fig. 77). Variation in this character among the specimens at hand is determined by the presence or absence of contact between the bony capsules containing Jacobson's organ and a median process of the maxillary bone. Initially, we distinguished complete septa formed by slender maxillary processes from complete septa formed by robust maxillary processes, but intermediate conditions made this additional refinement too arbitrary for confident scoring.

We scored the development of the canal transmitting the infraorbital nerve in the floor of the infraorbital foramen (fig. 78) using the numerical coding suggested by Patton (1987): no groove present (1), or groove moderately developed (2), or groove well defined (3). Scoring these conditions as well as intermediate states (1.5, 2.5) was accomplished by reference to exemplar specimens of Brazilian *Proechimys guyannensis* previously examined by J. L. Patton (personal commun.). Therefore, we presume that our

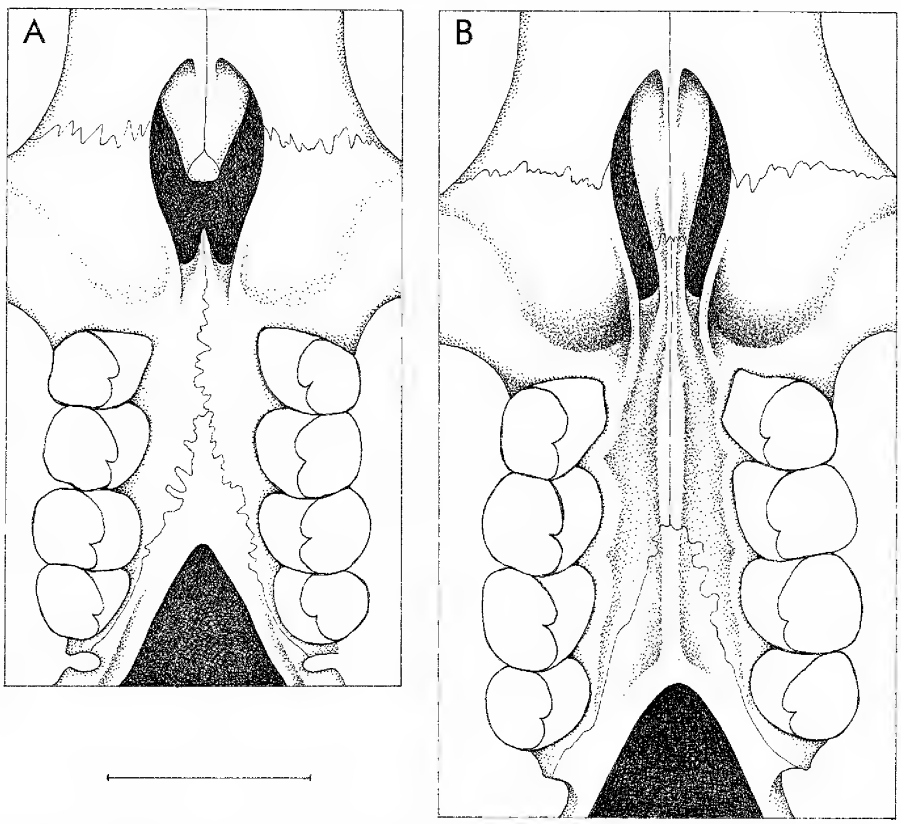

Fig. 77. Morphology of the incisive foramina and the posterior palate in *Proechimys guyannensis* (**A,** AMNH 266595) and *P. cuvieri* (**B,** AMNH 266592). Whereas the bony septum that separates the right and left incisive foramina is usually incomplete in *P. guyannensis,* the septum is always complete in *P. cuvieri.* Additionally, the incisive foramina of *P. cuvieri* are usually constricted posteriorly by well-developed lateral flanges of the maxillary bone, the posterior palate often has a prominent median keel, and the mesopterygoid fossa is typically broad and shallow. By contrast, the bony relief of the posterior palate is less prominent in most specimens of *P. guyannensis,* in which the mesopterygoid fossa is often narrower, more acutely angled, and penetrates farther between the toothrows. Scale bar = 5 mm.

trait-frequency data and his (Patton, 1987: table 3) are comparable.

We also followed Patton's (1987) numerical coding convention for the depth of the mesopterygoid fossa (fig. 77): not extending to the posterior margin of M3 (1), or extending to the posterior half of M3 (2), or extending to the anterior half of M3 (3), or extending to the posterior half of M2 (4), or extending to the anterior half of M2 (5). Because the angle formed by the posterior palatal margins of the mesopterygoid is correlated with the depth of penetration of the fossa between the toothrows (deeper fossae have more acutely angled palatal margins; Patton, 1987), we did not score the shape of the mesopterygoid notch as a separate character.

Finally, we recorded the number of internal folds on the second mandibular molar (corresponding to the "îlots d'émail" of Petter, 1978); compound (Y-shaped) folds were each counted as one-and-a-half folds. As noted by Patton (1987), internal fold number and morphology change with toothwear, so it is particularly important that this character be scored among individuals of approximately equivalent age.

Trait frequencies of these four qualitative characters differ significantly between our

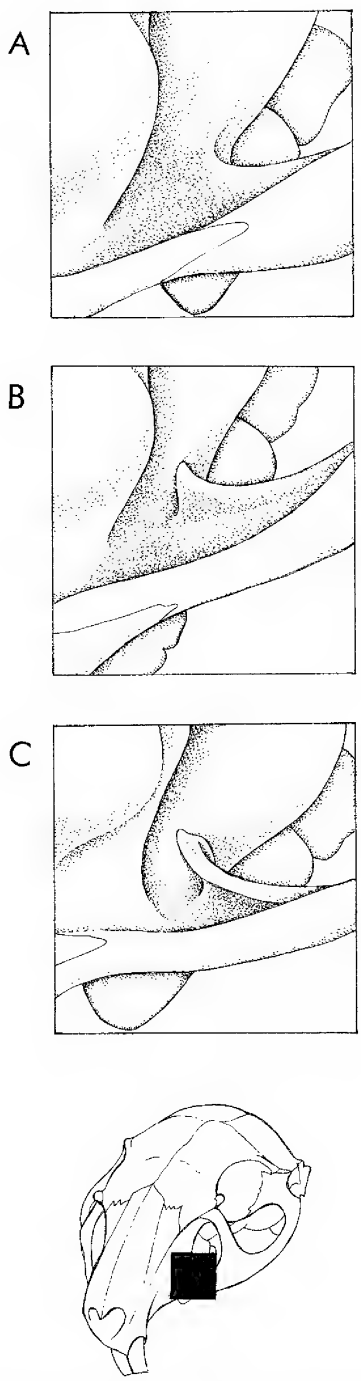

Fig. 78. Morphology of the floor of the infraorbital foramen in French Guianan *Proechimys,* illustrating alternative conditions of the canal for the infraorbital nerve scored as character states in table 46. **A,** Floor of infraorbital foramen smooth, without nerve canal (*P. cuvieri* [AMNH 266572] scored as "1"); **B,** nerve canal present, defined by moderately developed lateral flange (*P. cuvieri* [AMNH 266574] scored as "2"); **C,** nerve canal present, defined by highly developed lateral flange (*P. guyannensis* [AMNH 266595] scored as "3").

operationally defined samples of *cuvieri* (with MTR $\geq$ 8.2 mm) and *guyannensis* (with MTR $\leq$ 8.0 mm) despite the small number of *guyannensis* available for scoring (table 46). The presence or absence of a complete incisive septum and the development of an infraorbital groove are the two qualitative characters most consistently correlated with maxillary toothrow length: all large-toothed specimens (*cuvieri*) have a complete incisive septum and either lack an infraorbital groove entirely or have a very weakly defined groove; by contrast, most small-toothed specimens have an incomplete incisive septum and well-defined infraorbital grooves. Although most specimens of both tooth-size classes have a moderately deep mesopterygoid fossa and 2½ folds on m2, no specimens of small-toothed rats in our sample have either a very shallow mesopterygoid fossa or m2s with 3 folds. It is noteworthy that the qualitative traits of the specimen with a maxillary toothrow length of 8.0 mm (MNHN 1981.48, which could be interpreted as an outlier of either tooth-size class) link it unambiguously with *guyannensis,* and that specimens with "atypical" states for one qualitative character (e.g., AMNH 267047, a small-toothed animal that lacks any trace of an infraorbital groove) are not atypical in other qualitative respects. Altogether, these results strongly support the hypothesis that the discrete tooth-size classes associated with the names *cuvieri* and *guyannensis* represent valid species, a conclusion that is further bolstered by external, genitalic, and karyotypic comparisons.

As noted by Malcolm (1992), the tail of *Proechimys cuvieri* is visibly hairier than that of *P. guyannensis.* This difference is caused by the individual caudal hairs, which curve outward from beneath each epithelial scale in *P. cuvieri,* where they can easily be seen standing away from the caudal surface (fig. 79, left). By contrast, the individual hairs are appressed to the caudal surface in *P. guy-*

TABLE 46
Comparisons of Qualitative Character-State Frequencies Between *Proechimys cuvieri* and *P. guyannensis*[a]

	cuvieri	*guyannensis*
Incisive septum		
Complete	54	4
Incomplete	0	9
$p \ll 0.01$		
Infraorbital groove		
Score of 1.0	34	1
Score of 1.5	19	0
Score of 2.0	2	3
Score of 2.5	0	6
Score of 3.0	0	5
$p \ll 0.01$		
Mesopterygoid fossa		
Score of 1	6	0
Score of 2	20	0
Score of 3	28	8
Score of 4	1	7
$p \ll 0.01$		
Lower molars		
With 2 folds	4	6
With 2½ folds	29	9
With 3 folds	22	0
$p \ll 0.01$		

[a] Specimens scored for these comparisons were nonsenescent adults (age classes 8 or 9 of Patton and Rogers, 1983) from French Guiana. See text for scoring conventions and table 45 for specimens examined. All relevant tests of association (chi-square, likelihood ratios, Fisher's Exact Test) give essentially equivalent results with these data.

annensis, where they are difficult to see without magnification; in consequence, the tail appears to be smooth and naked (fig. 79, right).

The dorsal body pelage of *Proechimys cuvieri* is, on average, redder (more saturated) than the generally drab (grayish or yellowish brown) fur of *P. guyannensis,* but there is sufficient overlap in color among the specimens at hand that this contrast is useful for field identification only in combination with size and other characters. This seems to be the only significant species color difference in the material we examined. For example, we did not see any diagnostically useful differences in ventral fur color (pure white in most specimens of both species), tail pig-

Fig. 79. Caudal pelage of *Proechimys cuvieri* (left, AMNH 267029) and *P. guyannensis* (right, AMNH 267037). Tails of *cuvieri* are conspicuously hairier than those of *guyannensis,* an external difference that is useful for field identification of these sympatric congeners.

mentation (distinctly bicolored in most specimens of both species), or hindfoot markings.

The male genitalia differ strikingly in shape between *Proechimys cuvieri* and *P. guyannensis*. Whereas the penis of *cuvieri* is short and very broad, that of *guyannensis* is long and slender, an obvious contrast that is reflected in the highly divergent bacular morphologies illustrated by Patton (1987: figs. 5, 10) for members of his *cuvieri* and *guyannensis* species groups. Although this character cannot be used to identify most museum study skins (few of which have the penis attached), it is potentially useful for field identifications because the penis can be extruded by retracting the prepuce of live animals.

Karyotypic data recorded on skin tags of MNHN specimens indicate that different diploid counts are associated with the divergent morphological phenotypes described above and corroborate Petter's (1978) and Reig et al.'s (1979) taxonomic assignments. Thus, five French Guianan specimens that we examined with recorded karyotypes of 2N = 28 (MNHN 1972.639, 1974.263, 1974.266, 1981.36, 1998.315) represent the *cuvieri* morphotype, whereas two specimens that we examined with 2N = 40 (MNHN 1983.376, 1998.312) represent the *guyannensis* morphotype.

In the following species accounts we summarize diagnostic characters, comment on Husson's (1978) identifications of Surinamese material, and evaluate the probable geographic distribution of *Proechimys cuvieri* and *P. guyannensis* based on our assessment of character variation in the material at hand.

Proechimys cuvieri Petter

Figures 77–80

VOUCHER MATERIAL: AMNH 266570–266575, 266578, 266580–266582, 266588, 266589, 266591, 266592, 266594, 267025–267030, 267032, 267034, 267039, 267041, 267045, 267599, 267601–267603, 269122; MNHN 1998.685–1998.699. Total = 46 specimens.

IDENTIFICATION: Based on the preceding synthesis of character data from French Guianan material, adult specimens of *Proechimys cuvieri* can be characterized as large rats that contrast with adults of the smaller sympatric species *P. guyannensis* by their longer (≥8.2 mm) maxillary toothrows (versus ≤8.0 mm in *guyannensis*), complete incisive septum (vs. septum usually incomplete in *guyannensis*), incisive foramina with larger posterolateral flanges (vs. foramina usually with smaller flanges in *guyannensis*), palatal bridge with better developed median keel (vs. palate unkeeled or weakly keeled in *guyannensis*), infraorbital groove absent or usually weakly developed (vs. groove usually well developed in *guyannensis*), mesopterygoid fossa often shallow and broad (vs. deeper and narrower in many *guyannensis*), lower molars usually with more than two internal folds (vs. lower molars often with two folds in *guyannensis*), tail visibly hairier (vs. apparently smooth and naked in *guyannensis*), pelage often reddish (vs. drab in most *guyannensis*), penis short and very broad (vs. longer and narrower in *guyannensis*), and diploid karyotype with 28 chromosomes (vs. 2N = 40 in *guyannensis*).

In our experience, fully adult *Proechimys* in French Guiana can be identified to species in the field with considerable confidence using external measurements (e.g., hindfoot length, table 45) and the qualitative external traits described above. However, taxonomic assignments of juvenile and subadult *Proechimys* (with unmolted or incompletely molted soft, gray, immature pelage) are always problematic. Tooth impressions (Malcolm, 1992) and molecular markers (Steiner et al., 2000) are potentially useful tools for identifying young animals that should be incorporated in future field studies. Otherwise, many individuals will inevitably remain unidentified in ecological research based on nondestructive sampling, especially during the rainy season, when a considerable fraction of the population consists of young animals (Guillotin, 1982).

Specimens that we examined document the sympatry of *Proechimys cuvieri* and *P. guyannensis* at several localities in French Guiana, including Arataye, Cayenne, Florida, Montsinéry, and St.-Eugène, as well as Paracou. We presume that these species are also co-distributed elsewhere, certainly in Suri-

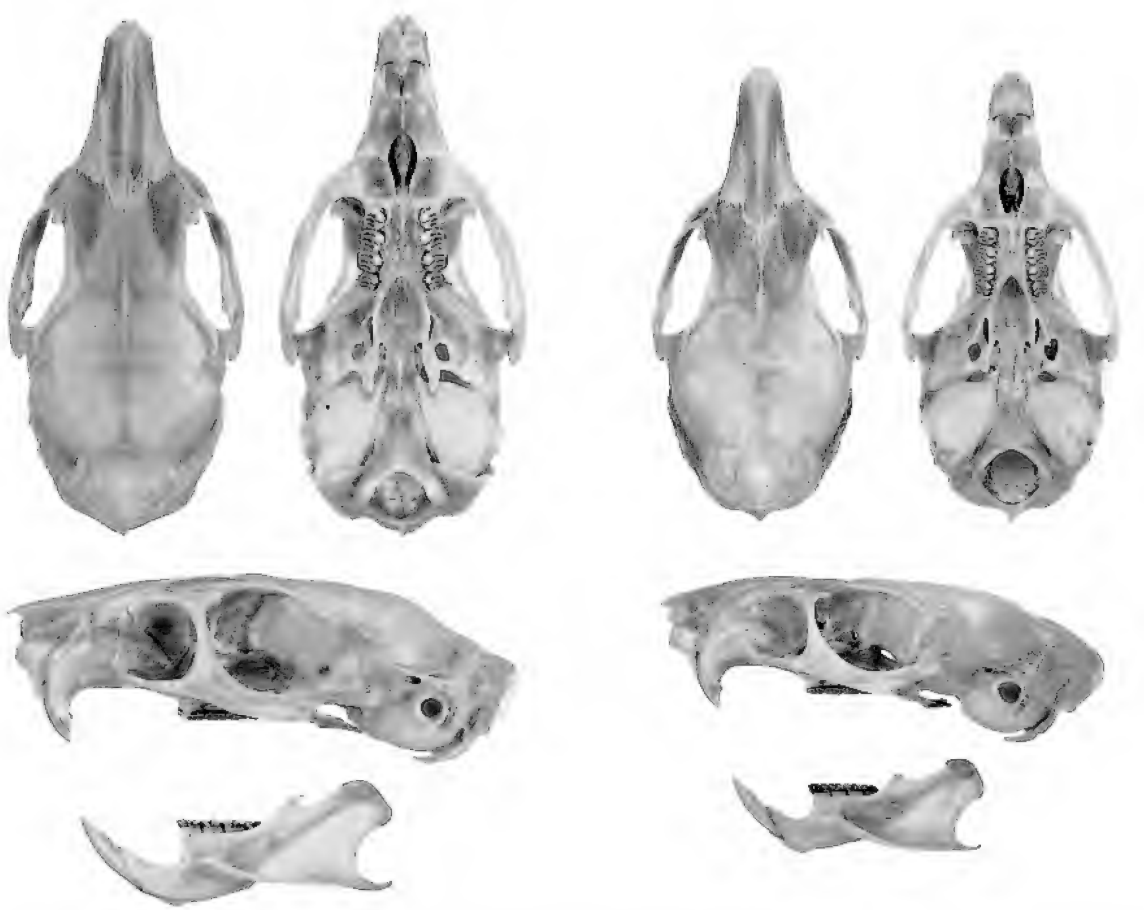

Fig. 80. Dorsal, ventral, and lateral views of skulls of *Proechimys cuvieri* (left, AMNH 266592) and *P. guyannensis* (right, AMNH 266595). All views approximately ×1.5.

nam and perhaps throughout the Guiana subregion of Amazonia.

According to Patton et al. (2000), *Proechimys cuvieri* is widely distributed in Amazonia, including large parts of the Guianan, southeastern, and western subregions. Although *cuvieri* is said to be relatively uniform in morphological characters throughout this enormous range, significant mtDNA sequence divergence (7–9%) exists among several geographic clusters of populations sampled by those authors (op. cit.). We have not attempted to evaluate geographic variation among Amazonian populations of *cuvieri*-like spiny rats for this faunal report, but it is relevant to note that typical (French Guianan) *cuvieri* appears to differ significantly from western Amazonian material in some morphological traits. For example, whereas Patton et al. (2000) reported that the vomer (an element of the incisive septum) is exposed in most (25 out of 34) specimens from the Rio Juruá, this bone is not exposed in any of our 22 adult Paracou vouchers. If geographic patterns of variation in this and other morphological characters were found to be consistently correlated with mtDNA haplotype divergence, it would be reasonable to infer that two or more species could be represented among the samples currently referred to this species.

REMARKS: Husson (1978) identified Surinamese material of this species as *Proechimys guyannensis* on the basis of Geoffroy's (1803) and Desmarest's (1817) color descriptions of the type, and on the assumption that the type of *guyannensis* probably represented the commoner of the two Guianan forms.

Color alone, however, is not a reliable basis for species identification, and the other morphological details mentioned in Geoffroy's and Desmarest's descriptions are likewise insufficient to determine which local species they had in hand. Petter's (1978) rediscovery of the long-lost type skull of *P. guyannensis* finally resolved the identity of that taxon and indicated the necessity of naming the larger form as a new species.

OTHER SPECIMENS EXAMINED: **French Guiana**—Arataye (MNHN 1983.378; USNM 548450–548452), Cacao (MNHN 1981.107), Cayenne (MNHN 1970.223, 1974.263), Florida (MNHN 1981.46, 1981.50), Piste St.-Élie (MNHN 1982.523), St.-Eugène (MNHN 1995.3220–1995.3222, 1995.3224, 1998.314, 1998.315, 1998.1821), Saül (MNHN 1977.774 [holotype], 1981.23, 1981.24, 1981.26, 1981.29–1981.33, 1981.36), Station FRG near Montsinéry (MNHN 1986.1129), Trois-Sauts (MNHN 1981.54, 1981.56), no other locality data (MNHN 1972.639, 1974.266).

FIELD OBSERVATIONS: All of our unambiguous records of *Proechimys cuvieri* from Paracou are based on collected specimens. Of our 46 vouchers, 18 (39%) were taken in Sherman traps, 14 (30%) were shot, 7 (15%) were taken in Victor traps, 4 (11%) were taken in Tomahawk traps, 2 (4%) were taken in Conibear traps, and 1 was taken in a pitfall. Forty-four specimens (96%) were shot or trapped at ground level, but 2 specimens (4%) were taken in traps tied to lianas 0.7–1.0 m above the ground. Habitat data recorded for 45 specimens include 10 captures (22%) in well-drained primary forest, 3 captures (7%) in swampy primary forest, 10 captures (22%) in creekside primary forest, 2 captures (4%) in primary forest of unspecified character, and 20 captures (44%) in secondary vegetation. Microhabitat notes accompanying 28 specimens trapped at ground level record captures made under masses of fallen branches and other debris (8 specimens), under logs (5), in unsheltered sites in dense understory vegetation (5), beside logs (3), at the bases of trees (2), among stilt roots (1), on top of a log (1), inside a hollow log (1), on a smooth branch fallen over a stream (1), and under an overhanging stream bank (1).

Proechimys guyannensis (E. Geoffroy)

Figures 77–80

VOUCHER MATERIAL: AMNH 266576, 266577, 266586, 266595, 267037, 267038, 267047; MNHN 1998.682–1998.684. Total = 10 specimens.

IDENTIFICATION: External and craniodental characters that distinguish this species from *Proechimys cuvieri* in French Guiana are discussed above and need not be repeated here.

Patton (1987) mapped the distribution of the *guyannensis* species group of *Proechimys* as extending throughout eastern Amazonia together with adjacent parts of the northern Venezuelan coast and the Brazilian Cerrado. Besides the type species, Patton listed the following taxa as group members: *cherriei* Thomas, *roberti* Thomas, *vacillator* Thomas, *oris* Thomas, *warreni* Thomas, *boimensis* Allen, *arescens* Osgood, *riparum* Moojen, and *arabupu* Moojen (see Cabrera, 1961, for bibliographic references). Patton believed that more than one valid species was represented by these names, emphasizing morphological differences between samples from the Guiana subregion (for which the oldest available name is *guyannensis*), and those from south of the Amazon (for which the oldest name is *roberti*).

The morphological trait frequencies reported herein for typical *Proechimys guyannensis* (from French Guiana) resemble those tabulated by Patton (1987) for *guyannensis*-group samples from north of the Amazon, which we provisionally regard as conspecific. By contrast, specimens from southeastern Amazonia have divergent trait frequencies (op. cit.) and also differ from north-bank samples in karyotypes and cytochrome-b sequences (Weksler et al., 2001). Apparently, all recently collected *Proechimys* from Venezuelan coastal rainforests (north of the Orinoco) are referable to other species groups (Aguilera and Corti, 1994; Aguilera et al., 1995; Corti and Aguilera, 1995). Therefore, *P. guyannensis* appears to be an Amazonian endemic largely, but perhaps not exclusively, distributed in the Guiana subregion.[23]

[23] The type locality of *Echimys cherriei* Thomas, a taxon listed by Patton (1987) as a member of the *guyannensis* species group, was incorrectly mapped (op. cit.: fig. 1) in the easternmost coastal rainforest region

REMARKS: Surinamese material of this species was identified as *Proechimys warreni* by Husson (1978), who used the name *P. guyannensis* for the larger species identified as *P. cuvieri* in this report (see the preceding account).

Although *Proechimys guyannensis* (Geoffroy, 1803) has long been recognized as a valid name (e.g., by Moojen, 1948; Hershkovitz, 1948b; Cabrera, 1961; Patton and Gardner, 1972; Patton, 1987), this epithet was rejected as unavailable by Woods (1993), who used the replacement name *cayennensis* Desmarest (1817) instead. In our opinion, *Mus guyannensis* and other names first published by Geoffroy (1803) are unambiguously available from that work for the reasons clearly explained by Hershkovitz (1955) and Holthuis (1963).

OTHER SPECIMENS EXAMINED: **French Guiana**—Arataye (MNHN 1983.381; USNM 548454–548456), Cayenne (MNHN 1983.374, 1983.376, 1995.1395 [holotype]), "Fleuve Oyapock" (MNHN 1983.375), Florida (MNHN 1981.48, 1982.601), Montsinéry (MNHN 1986.1124), Nancibo (MNHN 1986.1130), Petit Saut (MNHN 1998.312), St.-Eugène (MNHN 1994.128), no other locality data (MNHN 1981.88, 1981.103).

[33] ←
of northern Venezuela, where only *P. trinitatis* is currently known to occur (see range maps in Aguilera and Corti [1994], Aguilera et al. [1995], and Corti and Aguilera [1995]). In fact, the type locality of *cherriei* is Munduapo (= Monduapo according to Paynter, 1982), on the right bank of the upper Orinoco at 4°54′N, 67°48′W in the Guiana subregion of Amazonia.

Other concepts of *Proechimys guyannensis* are not consistent with the taxonomic and geographic limits recognized in this report. In particular, the synonymy of *P. cayennensis* (= *P. guyannensis* in our usage) provided by Woods (1993) includes *columbianus* Thomas (a member of Patton's [1987] *semispinosus* species group); *hylaea* Moojen, *leioprimna* Moojen, *nesiotes* Moojen, and *rattinus* Thomas (members of Patton's *goeldii* species group); *ochraceus* Osgood (a member of Patton's *trinitatus* species group); and *villacauda* Moojen (a member of Patton's *longicaudatus* species group). Apparently, Woods' association of these nominal taxa with *guyannensis* followed Moojen's (1948) generic revision, a historically important but now outdated reference. Unless shown to be incorrect by subsequent research, Patton's carefully documented allocations of nominal taxa to species groups should be used as the basis for all future classifications of *Proechimys.*

TABLE 47
Comparison of Capture-Habitat Frequencies between *Proechimys cuvieri* and *P. guyannensis* Trapped at Paracou[a]

	Capture habitat		
	Primary forest	Secondary growth	Totals
cuvieri	25	20	45
guyannensis	10	0	10
Totals	35	20	55
$\chi^2 = 7.0$, df = 1, $p < 0.01$			

[a] Table entries are numbers of captures. The chi-square value calculated from these data tests the null hypothesis of no interspecific difference in proportions of captures by habitat.

FIELD OBSERVATIONS: All of our definite records of *Proechimys guyannensis* at Paracou are based on collected specimens. Of our 10 vouchers, 3 (30%) were captured in Victor traps, 5 (50%) in Sherman traps, and 2 (20%) were shot. Eight of our vouchers (80%) were shot or trapped on the ground, but 2 (20%) were taken in traps tied to lianas 0.5–1.6 m above the ground. Recorded habitat data include 9 captures (90%) in well-drained primary forest and 1 (10%) in creekside primary forest. By comparison with *Proechimys cuvieri,* which we caught with almost equal frequency in primary forest and secondary growth, *P. guyannensis* was captured significantly more often in primary forest (table 47).

ANALYSES OF SAMPLING

We encountered nonvolant mammals on a daily basis at Paracou even when we made no deliberate effort to collect or observe them. Tamarins twittered and plunged in the canopy around our camp in the mornings, agoutis fled barking through the undergrowth at midday, kinkajous whistled above our bat nets at night, and armadillos bolted across the path as we returned to camp later in the evening. Therefore, every day we spent in the field was potentially informative as an interval of nonvolant mammal sampling, whether or not we cataloged specimens or recorded noteworthy sightings on a given date. Similarly, although no more than two persons were ever simultaneously committed

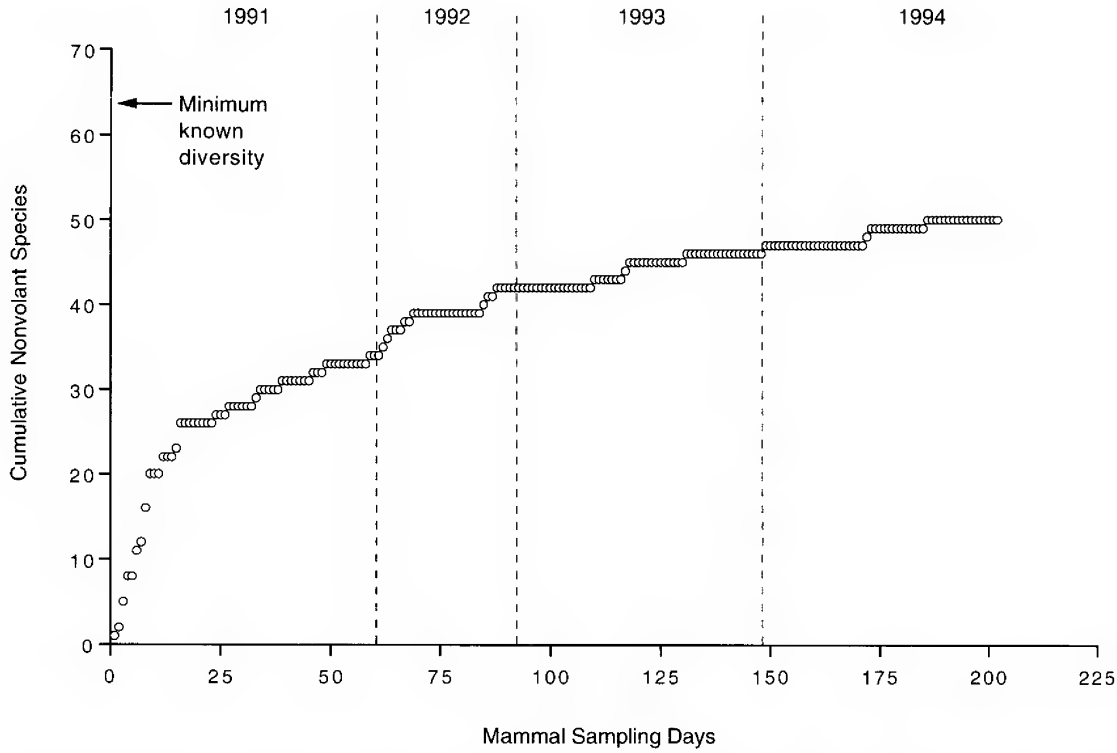

Fig. 81. Results of nonvolant mammal sampling at Paracou from 1991 to 1994, where we recorded a total of 50 species in 202 days using all direct methods of nonvolant faunal inventory (trapping, hunting/census, and miscellaneous; table 48). "Minimum known diversity" (64 species) includes the additional records obtained by previous researchers in our study area, together with second-hand observations that we documented by interviewing local residents.

to the nonvolant mammal survey, all inventory personnel made significant observations of nonvolant species from time to time. Because a substantial amount of diversity data thus accumulated involuntarily, it is difficult to quantify meaningfully the time or effort expended on the nonvolant mammal inventory at Paracou. In the absence of any better sampling units, however, field days can be used to obtain a general overview of our results.

Counting only those records—collected specimens and unvouchered observations—that resulted from our own efforts (excluding interview results; table 48), we documented the occurrence of 50 nonvolant species over the 202 dates that we worked in the field from 1991 to 1994. After an initially rapid rate of about 1.6 species/day in the first two weeks of 1991 (fig. 81), species accumulation abruptly levelled to around 0.2 species/day throughout the remainder of that field season and the next; in 1993 and 1994, the average rate of species accumulation was less than 0.1 species/day. Although these data suggest an approaching asymptote, field days were not commensurate units of sampling effort throughout the course of our inventory because different methods were used in different years, and because some methods were more effective, or were used more intensively, early in the inventory than later (table 49). Furthermore, the minimum known diversity of nonvolant mammals at Paracou (64 species, based on additional records from interviews and other sources) is so far above the levelling terminal portion of our graph as to suggest that the latter is misleading about completeness. Analyzing the results of each inventory method separately therefore provides a better picture of sampling effectiveness.

TABLE 48

Summary of Nonvolant Mammal Records at Paracou by Species and Method[a]

	Trapping			Hunting/census				
	Conventional	Arboreal	Pitfall	Diurnal	Nocturnal	Misc.	Total	Interviews[b]
Caluromys philander	0	8	0	0	10	0	18	—
Chironectes minimus	3	0	0	0	23	0	26	no
Didelphis marsupialis	14	1	0	0	8	0	23	—
Gracilinanus emiliae	0	0	0	0	1	0	1	—
Hyladelphys kalinowskii	0	0	2	0	1	0	3	—
Marmosa murina	0	0	0	0	3	2	5	—
Marmosops parvidens	2	0	7	0	6	0	15	—
Marmosops pinheiroi	3	0	12	0	4	0	19	—
Metachirus nudicaudatus	4	0	0	0	18	0	22	—
Micoureus demerarae	3	2	0	0	8	0	13	—
Monodelphis brevicaudata	1	0	0	0	0	0	1	—
Philander opossum	11	0	1	0	38	0	50	—
Bradypus tridactylus	0	0	0	0	0	0	0	yes
Choloepus didactylus	0	0	0	1	4	0	5	yes
Cabassous unicinctus	0	0	0	0	0	0	0	yes
Dasypus kappleri	0	0	0	0	3	0	3	—
Dasypus novemcinctus	0	0	0	some	many	0	many	—
Priodontes maximus	0	0	0	0	1	0	1	yes
Cyclopes didactylus	0	0	0	0	0	0	0	yes
Myrmecophaga tridactyla	0	0	0	0	0	0	0	yes
Tamandua tetradactyla	0	0	0	1	1	0	2	yes
Saguinus midas	0	0	0	many	0	0	many	yes
Alouatta seniculus	0	0	0	many	many	0	many	yes
Ateles paniscus	0	0	0	1	0	0	1	yes
Cebus apella	0	0	0	0	0	0	0	yes
Pithecia pithecia	0	0	0	3	0	0	3	yes
Saimiri sciureus	0	0	0	0	0	0	0	yes
Speothos venaticus	0	0	0	0	0	0	0	yes
Herpailurus yaguarondi	0	0	0	0	0	0	0	yes
Leopardus pardalis	0	0	0	0	0	0	0	yes
Leopardus wiedii	0	0	0	0	2	0	2	?
Panthera onca	0	0	0	0	0	1	1	yes
Puma concolor	0	0	0	0	0	0	0	yes
Eira barbara	0	0	0	3	0	0	3	yes
Galictis vittata	0	0	0	0	0	0	0	yes
Nasua nasua	0	0	0	2	1	0	3	yes
Potos flavus	0	0	0	0	many	0	many	yes
Tapirus terrestris	0	0	0	0	0	0	0	yes
Mazama americana	0	0	0	2	0	0	2	yes
Mazama gouazoubira	0	0	0	0	6	0	3	yes
Pecari tajacu	0	0	0	1	0	2	3	yes
Tayassu pecari	0	0	0	0	0	1	1	yes
Sciurillus pusillus	0	0	0	6	0	0	6	yes
Sciurus aestuans	2	0	0	20	0	0	22	yes
Neacomys dubosti	0	0	1	0	0	0	1	—
Neacomys paracou	20	0	8	0	1	0	29	—
Nectomys melanius	0	0	0	0	0	0	0	—
Neusticomys oyapocki	0	0	2	0	0	0	2	—
Oecomys auyantepui	4	3	0	0	0	0	7	—
Oecomys rutilus	2	1	7	0	2	0	12	—
Oligoryzomys fulvescens	0	0	0	0	3	0	3	—

TABLE 48—(*Continued*)

	Trapping			Hunting/census				
	Conventional	Arboreal	Pitfall	Diurnal	Nocturnal	Misc.	Total	Interviews[b]
Oryzomys macconnelli	0	0	0	0	0	0	0	—
Oryzomys megacephalus	30	0	1	0	5	0	36	—
Oryzomys yunganus	17	0	1	0	0	0	18	—
Rhipidomys nitela	0	2	1	0	0	4	7	—
Coendou melanurus	0	0	0	0	1	0	1	no
Coendou prehensilis	0	0	0	0	0	1	1	yes
Dasyprocta leporina	0	0	0	many	2	0	many	yes
Myoprocta acouchy	2	0	0	many	1	0	many	yes
Cuniculus paca	0	0	0	0	many	0	many	yes
Makalata didelphoides	0	0	0	1	0	0	1	—
Mesomys sp.	1	0	0	0	0	0	1	—
Proechimys cuvieri	31	0	1	0	14	0	46	—
Proechimys guyannensis	8	0	0	0	2	0	10	—

[a] Except as noted for interview results, table entries are numbers of collected specimens and/or recorded observations; "some" and "many" are subjective judgments of frequency of unrecorded observations for common species. Records based on incompletely identified specimens and observations (e.g., sightings of *Didelphis* spp., released juvenile *Proechimys* spp.) are not tabulated, nor are records based on specimens collected by previous researchers who worked at Paracou (e.g., *Nectomys melanius* and *Oryzomys macconnelli* trapped by O. Henry). Inventory methods are defined in the text, with the exception of "miscellaneous" (which includes records based on tracks, salvaged material, and specimens collected inside bat roosts).

[b] Interview results are tabulated only for species that could be retrospectively identified with certainty; we did not ask interviewees about taxa distinguished by characters that would not be obvious to untrained observers. Because the total number of observations on which interview responses were based was seldom known, only the presence or absence of positive knowledge of the species by interviewees is recorded here.

Sampling Results from Different Methods

None of the methods that we used to inventory the nonvolant mammal fauna at Paracou recorded all of the species known to occur in our study area. Instead, each method appeared to be maximally effective for some taxa and relatively ineffective for others. Below we summarize our principal sampling results method by method and explain some of the factors that affect our subsequent assessments of complementarity and completeness.

Conventional Trapping: Most conventional trapping at or near ground level (0–3 m by our convention) was accomplished in 1991 and 1992, when ten Victor/Sherman traplines were established at widely separated sites within our 3-km sampling radius. Whereas some Victor/Sherman traplines contained over 100 traps and extended for 2 km or more, most were shorter and contained fewer traps. The shortest interval that any Victor/Sherman trapline was operational was 8 nights, the longest interval was 14 nights, and the average interval was 12 nights. In total, we trapped on 71 dates in 1991 and 1992 with an average of 84 Victor/Sherman traps deployed per night. Supplementary ground-level trapping with other equipment (Tomahawks, Conibears, and legholds) was much more intensive in 1991 than in any subsequent year, but the numbers of supplementary traps deployed each night were not consistently recorded.

Combining results from conventional trapping with all commercially available equipment, we captured a total of 162 individuals representing 18 species of marsupials and rodents, including our only examples of *Monodelphis brevicaudata* and *Mesomys* sp. (table 48). Species accumulated quickly at first: we took 15 species in our first 74 captures, for an initial average rate of almost one new species per five individuals trapped (fig. 82). However, only three additional species were represented among the last 88 captures by

TABLE 49
Methods and Effort Used to Sample Nonvolant Mammal Diversity at Paracou, 1991–1994

	Field days	Trapping[a]			Hunting/census[b]	
		Conventional	Arboreal	Pitfall	Diurnal	Nocturnal
1991	61	3633 TN	no	no	yes	ca. 350 hr
1992	30	2327 TN	no	no	yes	96.7 hr
1993	57	<100 TN	2004 TN	2783 BN	yes	79.2 hr
1994	54	<100 TN	no	no	yes	64.4 hr

[a] Tabulated units of effort are trap-nights (TN) for conventional trapping (only Victor/Sherman trapping effort was quantified) and arboreal trapping, or bucket-nights (BN) for pitfall trapping.

[b] Diurnal hunting/census effort was not consistently quantified. Nocturnal hunting effort was estimated (for 1991) or recorded (1992–1994) in hours (hr).

this method, or about one new species per 30 individuals trapped.

In general, Victors and Shermans took smaller species than did Tomahawks, Conibears, and legholds (fig. 83), but there was some taxonomic overlap (table 50). For example, both classes of traps commonly took adult *Proechimys,* and juveniles of some large marsupials (e.g., *Didelphis marsupialis, Metachirus nudicaudatus, Philander opossum*) usually taken in Tomahawks and Conibears were also occasionally taken in Victors. However, Victors and Shermans never captured squirrels or any adult individuals of *Didelphis, Metachirus, Philander,* or *Myoprocta.* Similarly, Tomahawks, Conibears, and legholds never took *Marmosops, Monodelphis, Neacomys, Oryzomys,* or *Mesomys* at Paracou. Therefore, both kinds of equipment provided useful information about local diversity.

The unimpressive numbers of individuals

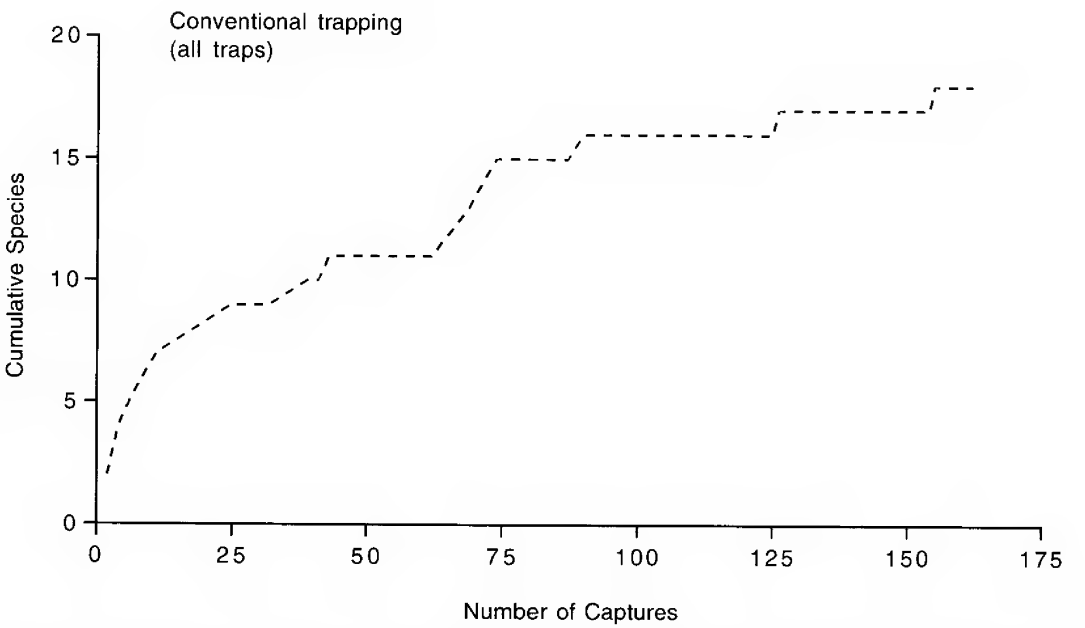

Fig. 82. Results of conventional trapping for nonvolant mammals at Paracou, using all commercially available equipment (Victor rat traps, Sherman live traps, Tomahawks, Conibears, and legholds) at or near ground level (0–3 m above the ground). A total of 162 captures representing 18 species of marsupials and rodents were recorded from 1991 to 1994.

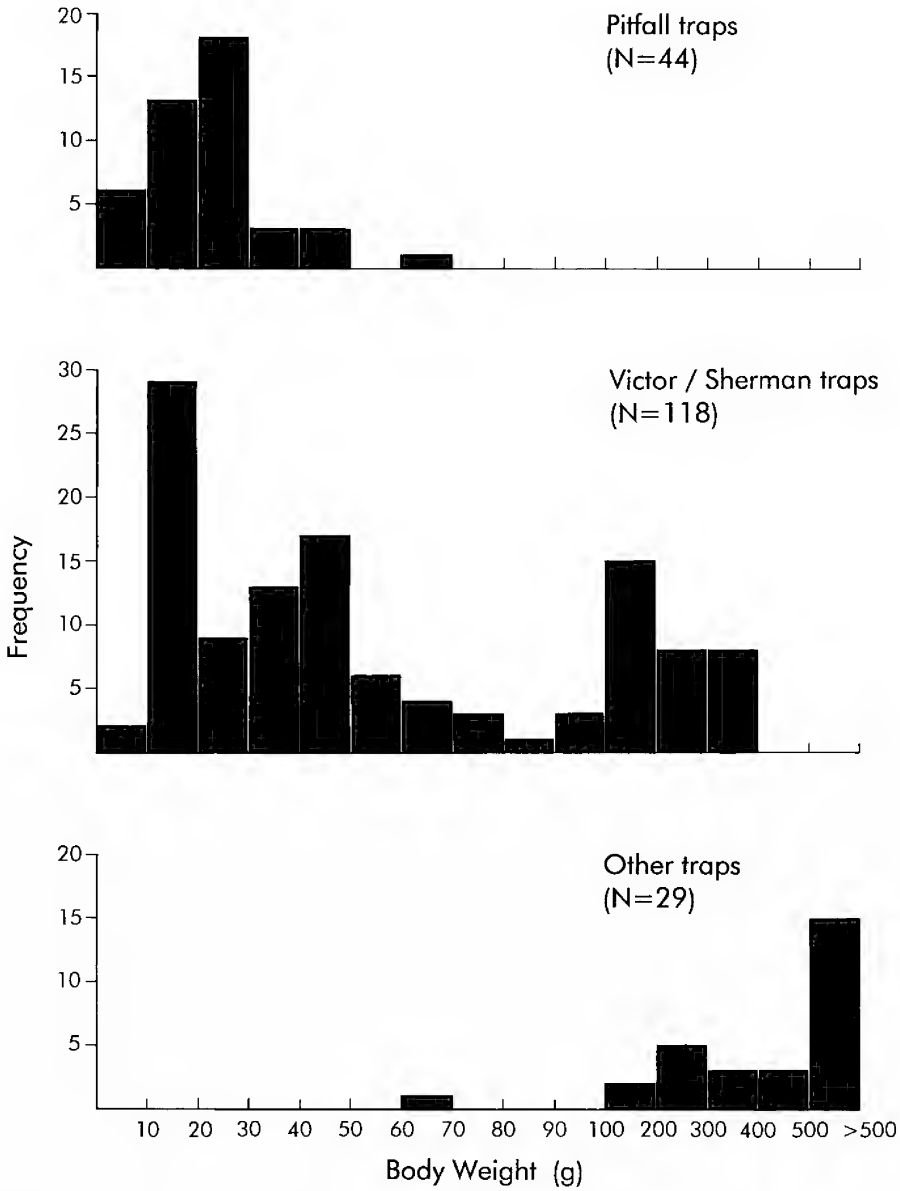

Fig. 83. Frequency histograms of body weights of nonvolant mammals (marsupials and rodents) taken at or near ground level by different trapping methods. Sample sizes (N) are recorded weights, which were not obtainable from all trapped individuals. "Other traps" includes captures made using Tomahawks, Conibears, and legholds (combined with Victor/Sherman captures in the first column of table 48).

captured by conventional trapping at Paracou is explained by a dramatic decline in trap success that we experienced over the course of our inventory. This phenomenon is best illustrated by the results obtained with Victor and Sherman traps, for which accurate counts of the numbers set each night are available. In effect, trap success (fig. 84, indicated by the slope of the solid line in the upper graph) changed abruptly when, after about 2600 trap-nights in 1991, traplines previously deployed for general collecting in productive habitats (e.g., well-drained primary forest) were shifted to less productive sites (e.g.,

TABLE 50
Frequency Data for Species Taken at Ground Level in Different Conventional Trap Types at Paracou[a]

	Victor/ Sherman traps	Other traps	Totals
Chironectes minimus	0	3	3
Didelphis marsupialis	1	13	14
Marmosops parvidens	2	0	2
Marmosops pinheiroi	3	0	3
Metachirus nudicaudatus	3	1	4
Micoureus demerarae	3	0	3
Monodelphis brevicaudata	1	0	1
Philander opossum	5	6	11
Sciurus aestuans	0	2	2
Neacomys paracou	20	0	20
Neacomys sp.[b]	2	0	2
Oecomys auyantepui	4	0	4
Oecomys rutilus	2	0	2
Oryzomys megacephalus	30	0	30
Oryzomys yunganus	17	0	17
Oryzomys sp.[c]	2	0	2
Myoprocta acouchy	1	1	2
Mesomys sp.	1	0	1
Proechimys cuvieri	25	6	31
Proechimys guyannensis	8	0	8
Totals	130	32	162

[a] Table entries are numbers of captures. "Other" traps include Tomahawks, Conibears, and legholds (see Materials and Methods).

[b] Escaped.

[c] Released juveniles.

along streams) and baited for certain target species expected to occur there. Furthermore, trap success in comparable situations was never as high in subsequent field seasons as it was in 1991. For example, we made 3.6 captures per 100 trap-nights using Victor and Sherman traps for general collecting in primary forest in 1991, but only 0.6 captures per 100 trap-nights using the same equipment in the same habitat in 1992 (an 83% decline). In total, we recorded only 128 captures in 5960 Victor/Sherman trap-nights at Paracou, for an overall success rate (captures per trap-night × 100) of 2.1%.

Species accumulation plotted against captures for Victor/Sherman trapping (fig. 84, lower graph) shows no sign of an asymptote despite the flattening terminal portion of the analogous graph for all conventional trapping combined (fig. 82). This paradox refects the late appearance in Victor traps of juvenile individuals of two species (*Didelphis marsupialis, Myoprocta acouchy*) previously taken only in Tomahawks, Conibears, or legholds, together with new taxa not taken by any other method (*Monodelphis* and *Mesomys*). Clearly, the apparent completeness of Victor/Sherman species sampling as assessed by trap-nights (fig. 84, dashed line in upper graph) is just an artifact of declining trap success.

ARBOREAL TRAPPING: We used arboreal platform traps only in 1993, when 25 trapping stations were established at approximately 20-m intervals along a transect through both well-drained and swampy primary forest. Trapping platforms were installed between 7.2 m and 19 m above the ground, with an average platform height of 13.7 m. From the date when the first arboreal trap station was operational (29 July) to the date when all platform trapping was discontinued (15 September), we trapped continuously for 47 nights with an average of 21 trapping stations operational per night. In total, we logged 1002 station-nights, which is equivalent to 2004 trap-nights if both Shermans and Tomahawks are counted. Seventeen individual marsupials and rodents were captured, for an overall success rate (captures per trap-night × 100) of only 0.8%.

Our 17 arboreal trap captures represent six species, none of which were taken exclusively by this method (table 48). The temporal pattern of captures (fig. 85, solid line in upper graph) suggests that traps were avoided for the first two weeks after installation (our first arboreal capture was made after 454 trap-nights) and that more prolonged trapping could have resulted in many more captures (trap success was higher in the last week of operation than in any previous interval). Although species accumulation plotted against captures (fig. 85, bottom graph) shows some indication of levelling, the number of individuals taken is too small to plausibly suggest any asymptotic value for taxonomic diversity obtainable by this method.

PITFALL TRAPPING: This method was used only in 1993, when five pitfall traplines were installed at widely separated locations in our study area: two in well-drained primary for-

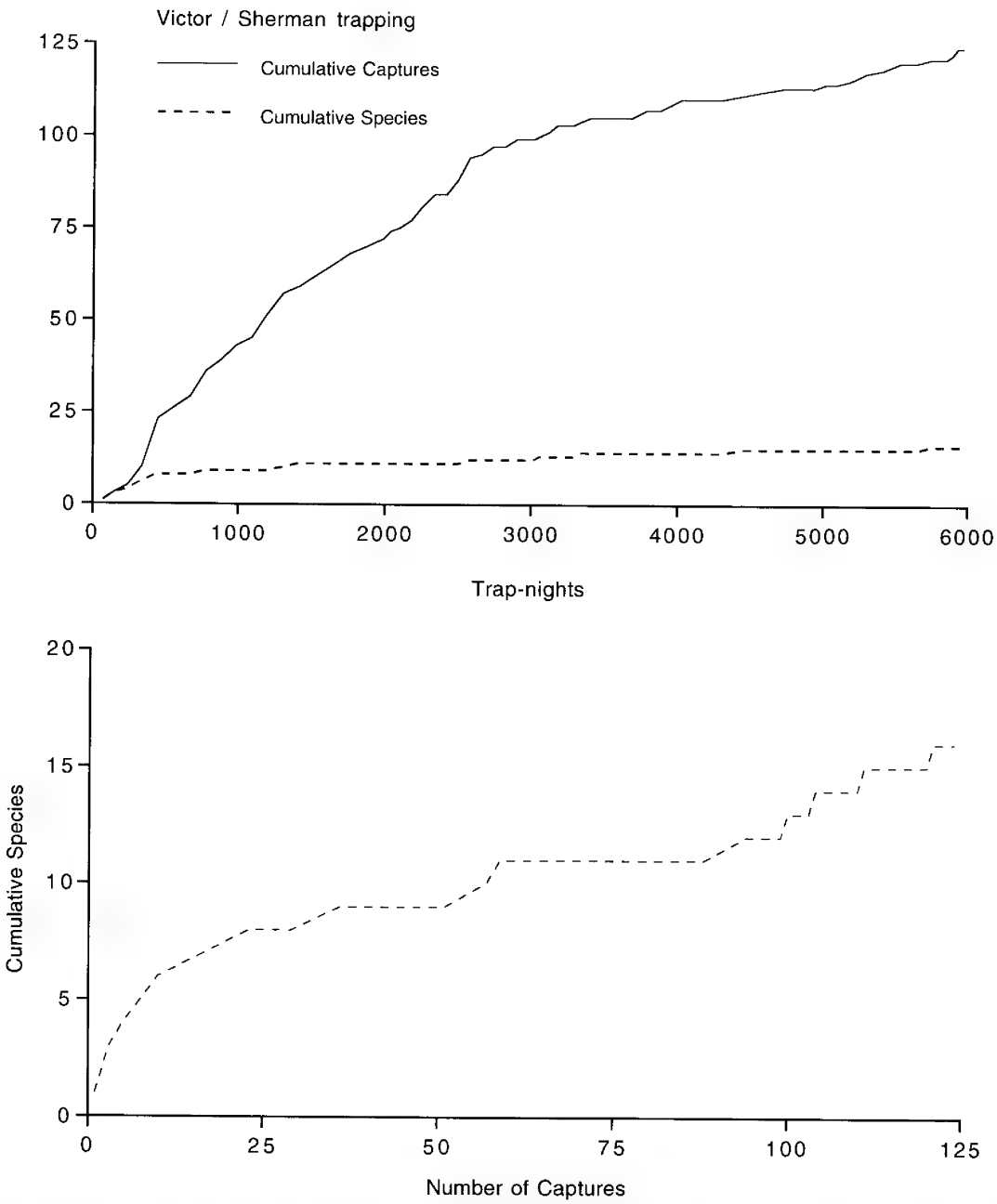

Fig. 84. Results of ground-level (conventional) trapping with Victor rat traps and Sherman live traps at Paracou, where 124 identifiable captures of 16 species of marsupials and rodents were obtained with 5960 trap-nights of effort using this equipment in 1991 and 1992. Note the abrupt change of slope for cumulative captures after about 2600 trap-nights in the upper graph.

est, one in swampy primary forest, and two in creekside primary forest. From the date when the first pitfall trapline was operational (21 July) to the date when all pitfalls were taken up (13 September), we trapped for 54 consecutive nights. Except for the first week of trapping (when the lines were still being installed), 55 buckets per night (11 in each

line) were deployed as pitfalls throughout this interval. In total, we logged 2783 bucket-nights and captured 45 individual mammals, for an overall success rate (captures per bucket-night × 100) of 1.6%.

Our 45 mammalian pitfall captures[24] represent 12 species of marsupials and rodents, of which two (*Neacomys dubosti* and *Neusticomys oyapocki*) were not taken by any other method (table 48). Most individual mammals captured in pitfalls were small, the great majority (84%) weighing less than 30 g (fig. 83). Pitfall captures accumulated rapidly in the first few weeks of trapping (fig. 86, solid line in upper graph), when we recorded about three captures per 100 bucket-nights on average; thereafter, our capture rate declined to a more-or-less steady rate of about 0.8 captures per 100 bucket-nights. Although species accumulation plotted against bucket-nights (fig. 86, dashed line in upper graph) suggests that faunal sampling with pitfalls was nearly complete, species accumulation plotted against captures (fig. 86, lower graph) does not show a convincing asymptote.

Diurnal Hunting: Because most of our sightings and collections of diurnal mammals resulted from chance encounters, sampling effort is hard to quantify for this method. On average, all inventory personnel spent at least several daylight hours in the forest per calendar date, so the total accumulation of time available for diurnal mammal observations was considerable: about 2500 hours (634 person-days × 4 hours/person-day) is a plausible estimate. However, much of the time that we spent in the forest by day was not conducive to observing cryptic species (e.g., sloths and pygmy squirrels), nor were all personnel alert to fleeting encounters with wary taxa locally persecuted as game (e.g., deer and monkeys). Given these and other problems with quantifying observational effort, field days are probably no worse than any alternative unit.

Diurnal mammal sightings accumulated at an initially rapid rate during our first several weeks at Paracou, but few new species were subsequently recorded by this method (fig. 87. Over the entire course of our inventory, we recorded 16 species from diurnal sightings (table 48). Although many of these were not found by us using other inventory methods, most were previously known to the local residents whom we interviewed. Oddly enough, the only species uniquely recorded by a diurnal observation was the usually nocturnal rodent *Makalata didelphoides.*

Nocturnal Hunting: Most of our observations and collections of nonvolant nocturnal mammals resulted from deliberate hunting (including sight censuses when few or no specimens were taken). Unfortunately, the duration of nightly hunts was not quantified in 1991 when this method was used most intensively. However, an estimate can be based on the fact that RSV and DPL both hunted every night on 58 consecutive dates in that year; assuming a typical hunt duration of 3.0 hours (the known average for hunts by the same personnel in 1992) yields a probable total effort of about 350 hours devoted to this method in 1991. Hunt durations were consistently recorded in subsequent field seasons: we devoted 96.7 hours to this method in 1992, 79.2 hours in 1993, and 64.4 hours in 1994. In total, we systematically hunted at night on 123 dates from 1991 to 1994 at Paracou, for a total cumulative effort of about 590 hours.

Nevertheless, chance observations made while bat netting contributed so many important records of nonvolant mammals (including our first of *Caluromys philander, Hyladelphys kalinowskii, Oligoryzomys fulvescens,* and *Priodontes maximus*) that it is misleading to ignore this source of nocturnal observations. Indeed, whereas our deliberate hunting effort per field season declined from 1991 to 1994, our bat netting effort increased in almost direct proportion (all inventory personnel were usually engaged in one activ-

[24] Among the many amphibians and reptiles captured in pitfall traps at Paracou were examples of *Leptodactylus* sp., *Bufo* cf. *typhonius, Otophryne pyburni, Caecilia tentaculata, Rhinatrema bivittatum, Coelodactylus amazonicus, Gonatodes annularis, Anolis chrysolepis, Plica plica, Plica umbra, Mabuya* sp., *Ameiva ameiva, Kentropyx calcarata, Arthrosaura kockii, Bachia flavescens, Iphisa elegans, Leposoma guianense, Neusticurus bicarinatus, Neusticurus rudis, Tretioscincus agilis, Amphisbaena fuliginosa, Typhlops reticulatus, Atractus* sp., *Erythrolamprus aesculapii, Helicops angulatus, Liophis* sp., *Oxyrhopus* sp., *Pseustes poecilonotus, Umbrivaga* sp., and *Leptomicrurus collaris.* Voucher material of these taxa (as provisionally identified by J. A. Campbell, C. J. Cole, and D. R. Frost) are preserved in the AMNH Department of Herpetology.

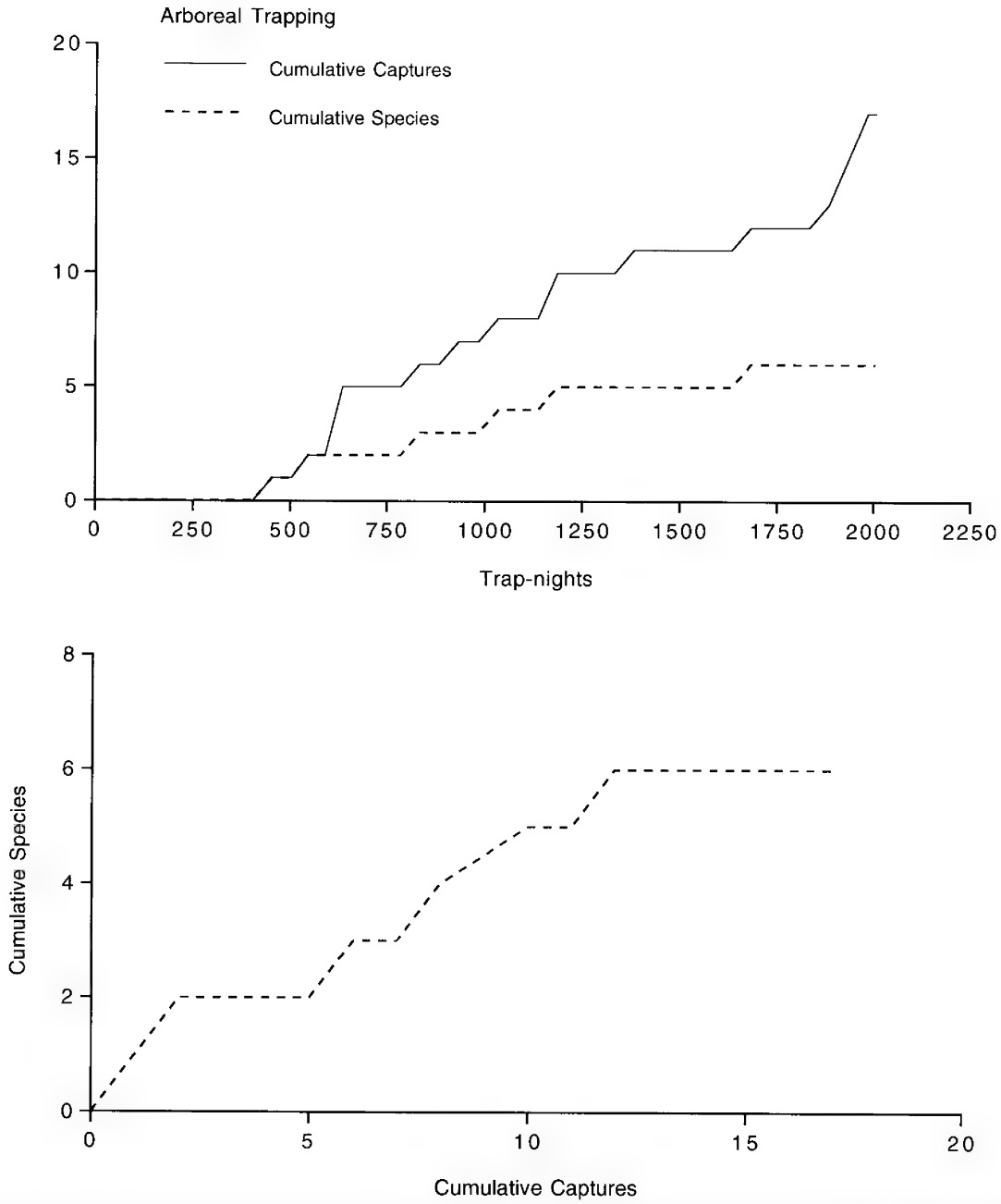

Fig. 85. Results of arboreal platform trapping at Paracou, where 17 captures representing six species of marsupials and rodents were obtained with 2004 trap-nights of effort in 1993.

ity or the other after dusk, seldom returning to camp before midnight), so the total time actually or potentially available to observe nonvolant nocturnal mammals per field date probably remained more-or-less constant throughout our inventory. It therefore makes sense to plot species accumulation by nocturnal observation as a function of calendar dates rather than dedicated search time (fig. 87, solid line).

Over the 202 dates that we worked at Paracou from 1991 to 1994, we recorded 31 spe-

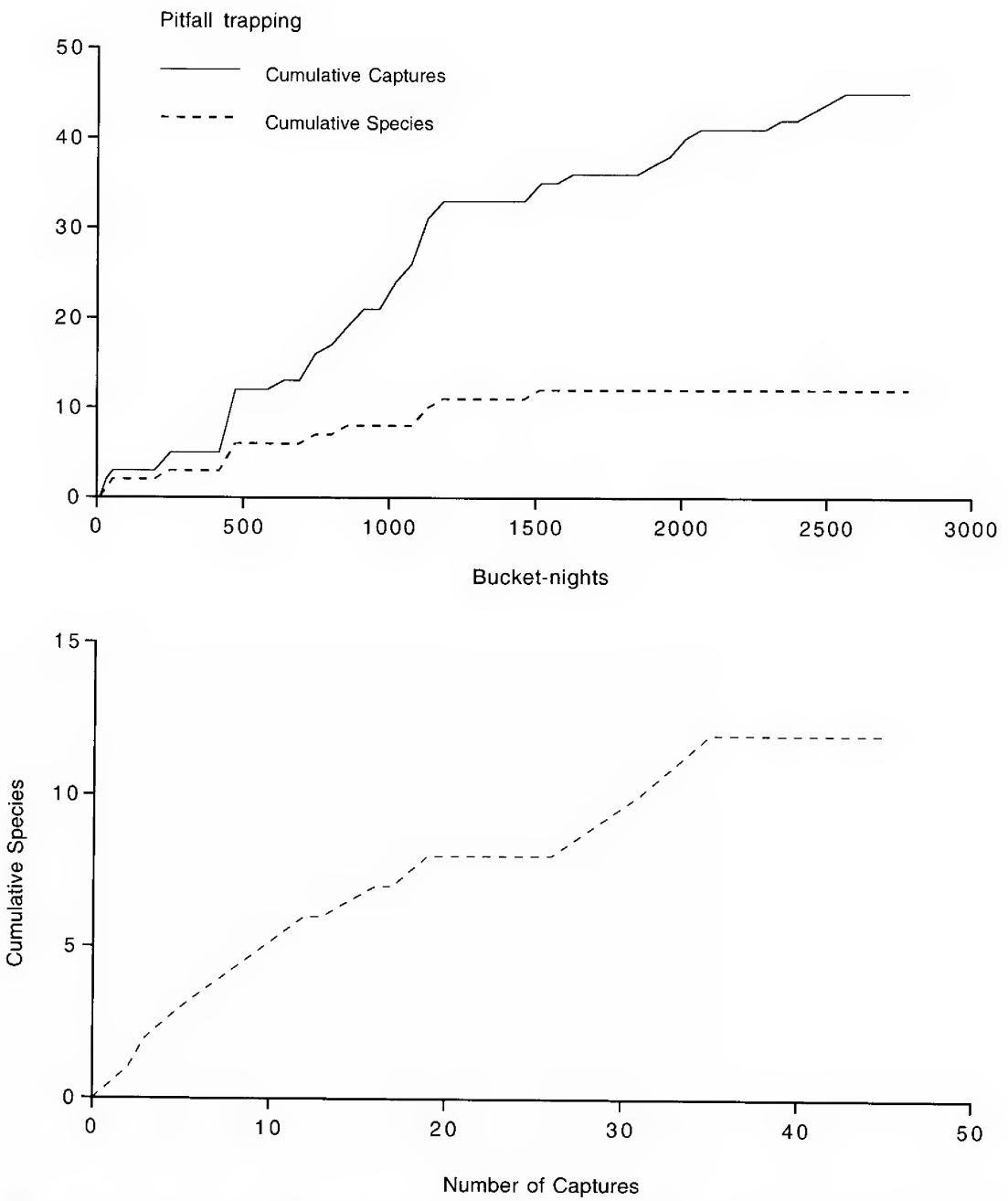

Fig. 86. Results of pitfall trapping at Paracou, where 45 captures representing 12 species of marsupials and rodents were recorded with 2783 bucket-nights of effort in 1993.

cies of nonvolant mammals by nocturnal observation, five of which were not recorded by any other method (*Gracilinanus emiliae, Dasypus kappleri, Leopardus wiedii, Oligoryzomys fulvescens, Coendou melanurus*; table 48). Although our rate of species accumulation by nocturnal observation was steepest in the first several weeks and decreased subsequently, no convincing asymptotic value is indicated. In total, we recorded 271 nocturnal observations that were unambiguously identifiable to species, but this sum

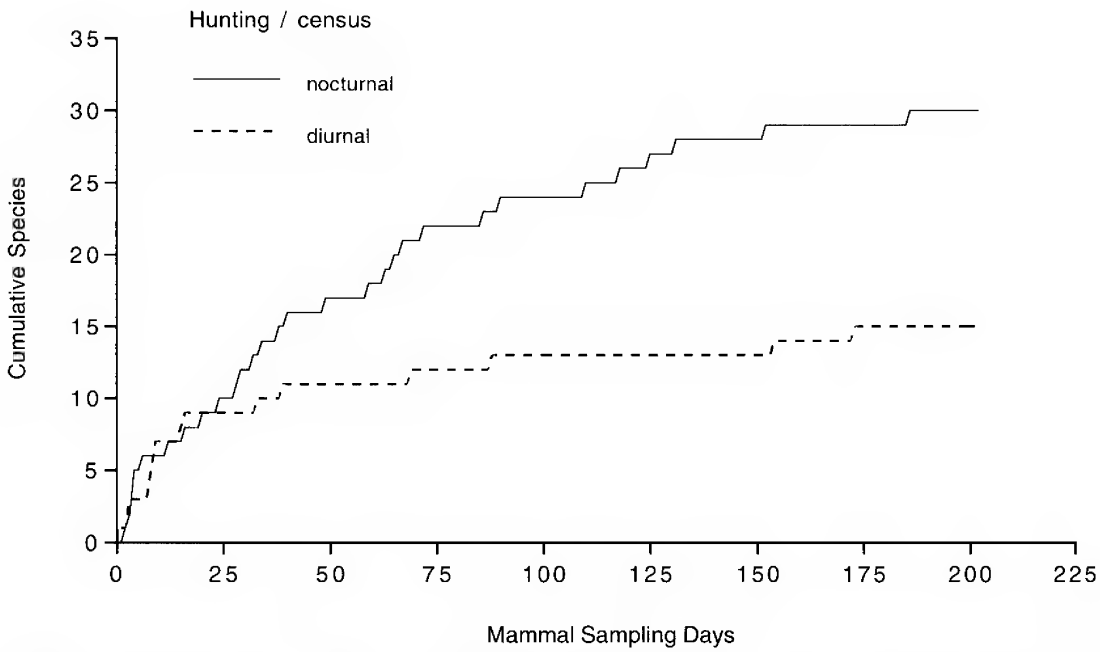

Fig. 87. Results of diurnal and nocturnal hunting/census at Paracou, where 16 species of nonvolant mammals were recorded by the former method and 31 species by the latter. In lieu of more appropriate measures of effort (see text), we simply plot species accumulation against field dates (202 total) for both methods.

does not include numerous unvouchered observations (mostly of common taxa) from 1991, nor did we record chance encounters with common species while bat netting. Therefore, only the smaller frequency classes for this method (table 48) represent accurate counts.

More interpretable frequency data were obtained from 1992 to 1994, when every identifiable observation (including sightings and distinctive sounds, except howler monkey vocalizations) were recorded in the course of 240.3 hours of systematic nocturnal hunting (table 51). Unidentified sightings and sounds (e.g., distant eyeshine, crashing noises in the undergrowth) were not consistently recorded. On average, we made 1.1 identifiable observations per hour of nighttime hunting from 1992 to 1994, a rate that did not differ substantially among the four persons principally involved in this activity (RSV, DPL, R. W. Kays, and L. H. Emmons).

Most identifiable nocturnal observations at Paracou represent a few common species with bright eyeshine, distinctive vocalizations, and/or noisy habits. Thus, records of *Potos flavus, Cuniculus paca, Philander opossum,* and *Chironectes minimus* account for over half of the data in table 51. By contrast, ten species represented by only one record each include some that may be genuinely uncommon, but others that are simply inconspicuous (silent, small, and/or with weak eyeshine), difficult to identify without specimens in hand, or usually diurnal (e.g., *Gracilinanus emiliae, Marmosa murina, Nasua nasua, Neacomys paracou, Oecomys rutilus, Oryzomys megacephalus, Proechimys guyannensis, Myoprocta acouchy*).

INTERVIEWS: Interviews resulted in 33 positive identifications of local species, of which 12 were not recorded by any other method (*Bradypus tridactylus, Cabassous unicinctus, Cyclopes didactylus, Myrmecophaga tridactyla, Cebus apella, Saimiri sciureus, Speothos venaticus, Herpailurus yagouarondi, Leopardus pardalis, Puma concolor, Galictis vittata, Tapirus terrestris*; table 48). Most of the species uniquely recorded from interviews are either uncommon throughout the Neotropics (e.g., *Cabassous unicinctus, Galictis vittata*) or are locally uncommon from

TABLE 51
Nocturnal Hunting/Census Results, 1992–1994

Taxon	Records[a]
Potos flavus	74
Cuniculus paca	26
Philander opossum	23
Chironectes minimus	17
Unidentified *Proechimys*	14
Unidentified *Dasypus*	11
Metachirus nudicaudatus	10
Proechimys cuvieri	10
Dasypus novemcinctus	8
Unidentified small marsupials	8
Mazama gouazoubira	5
Unidentified mice on ground	5
Caluromys philander	4
Alouatta seniculus[b]	4
Unidentified *Didelphis*	4
Unidentified mice in trees	4
Marmosops parvidens	3
Marmosops pinheiroi	3
Unidentified *Marmosops*	3
Micoureus demerarae	2
Choloepus didactylus	2
Dasypus kappleri	2
Leopardus wiedii	2
Dasyprocta leporina	2
Unidentified *Mazama*	2
Didelphis marsupialis	1
Gracilinanus emiliae	1
Marmosa murina	1
Tamandua tetradactyla	1
Nasua nasua	1
Neacomys paracou	1
Oecomys rutilus	1
Oryzomys megacephalus	1
Proechimys guyannensis	1
Myoprocta acouchy	1
Unidentified large cat	1
Unidentified small cat	1
Total records	260

[a] Observations systematically recorded in fieldnotes while hunting at night (240.3 hours total). Observations recorded haphazardly in the course of other nocturnal activities (e.g., bat netting) are not included. Two or more conspecific individuals observed simultaneously (e.g., mother/offspring pairs or other social groups) are counted as single records.

[b] Vocalizations only; commonly heard at night but seldom recorded.

overhunting (e.g., *Cebus apella, Tapirus terrestris*); others, however, are perhaps common but seldom seen because they are cryptic (e.g., *Bradypus tridactylus*) or wary (e.g., *Leopardus pardalis*). Only two relatively large and easily identified local species (*Chironectes minimus, Coendou melanurus*) were not familiar to our interviewees.

Although interviewees often estimated the relative frequency with which mammals were observed (e.g., see accounts for *Bradypus tridactylus* and *Mazama gouazoubira,* above), accurate counts of second-hand observations were only available for the rarest species. Interview records known to have been based on single observations include those for *Cabassous unicinctus, Priodontes maximus, Pithecia pithecia, Saimiri sciureus,* and *Galictis vittata.* Only two second-hand observations are known for *Cyclopes didactylus* and *Nasua nasua*; three for *Speothos venaticus* and *Leopardus pardalis*; and four for *Myrmecophaga tridactyla, Panthera onca,* and *Puma concolor.*

SUMMARY: Although each inventory method that we used to sample nonvolant mammal diversity at Paracou produced a different list of species, some methods were clearly more productive and/or produced more distinctive lists than others. Relevant quantitative comparisons (table 52) include the total number of species recorded by each method, the number of unique species, and pairwise complementarity values. The latter reflect the extent to which two methods provide nonredundant diversity information: low complementarity values imply high redundancy, whereas high complementarity implies low redundancy (see table footnote for computational details).

Clearly, interviews produced more species records (33) than any other single method used in our nonvolant inventory, as well as the largest number (12) and proportion (36%) of unique species. Nocturnal hunting ranks next by these criteria, followed by conventional trapping. Pitfall trapping and diurnal hunting each recorded some unique species, but arboreal trapping did not and was also least productive in terms of total records.

The lowest complementarity value calculated from our sampling data (60%) corresponds to the comparison of diurnal hunting with interviews, methods that were substantially redundant for the obvious reason that almost all diurnally active mammals at Par-

TABLE 52
Quantitative Comparisons of Six Nonvolant Mammal Inventory Methods Used at Paracou

Method	Recorded species		Percent complementarity[a]					
	Total	Unique						
Conventional trapping (CT)	18	2	—					
Arboreal trapping (AT)	6	0	80	—				
Pitfall trapping (PT)	12	2	64	88	—			
Diurnal hunting (DH)	16	1	94	100	100	—		
Nocturnal hunting (NH)	31	5	64	88	77	82	—	
Interviews (IN)	33	12	96	100	100	60	82	—
			CT	AT	PT	DH	NH	IN

[a] We define complementarity (after Colwell and Coddington, 1994) as the fraction of all species recorded by two methods that were recorded by only one or the other of them. Algebraically, if S_j and S_k are the number of species recorded by methods j and k, respectively, and if V_{jk} is the number of species recorded by both methods, then the complementarity between methods j and k is calculated as the quotient $C_{jk} = U_{jk}/S_{jk}$, where $U_{jk} = S_j + S_k - 2V_{jk}$ and $S_{jk} = S_j + S_k - V_{jk}$. Therefore, two methods with nonoverlapping species lists have a complementarity of unity, and two methods with identical species lists have a complementarity of zero. We calculated percent complementarity as the product $C_{jk} \times 100$.

acou were known to local inhabitants. Similarly, the second-lowest complementarity value we computed (64%) corresponds to the comparison of pitfall trapping with conventional trapping, methods that produced broadly overlapping lists of small marsupials and rodents. By contrast, other pairs of methods (such as pitfall trapping and interviews on the one hand, or arboreal trapping and diurnal hunting on the other) are 100% complementary because they produced no recorded species in common.

Overall, 22 species were each recorded by only one of the six methods we used to sample the nonvolant fauna at Paracou. If the two species uniquely taken in conventional traps by previous researchers (*Nectomys melanius, Oryzomys macconnelli*) are added to this total, then about 38% of the known nonvolant fauna (64 species) were recorded by a single method each. If miscellaneous records (e.g., scavenged material, occasional observations of distinctive spoor) are discounted for an additional four species (*Marmosa murina, Panthera onca, Tayassu pecari, Coendou prehensilis*; table 48), then a total of 28 species (44% of the known fauna) was not redundantly recorded. Of the 36 redundantly recorded species, 20 were recorded by two methods each, 14 by three methods, and 2 by four methods.

Estimating Completeness

Because none of our species accumulation graphs shows a convincing asymptote, it is reasonable to expect that more species could have been recorded with additional sampling effort by each method. Visual comparisons of these graphs, however, suggest that asymptotic values for species accumulation may have been more closely approached by some methods (e.g., conventional trapping, fig. 82) than by others (e.g., pitfall trapping, fig. 86). In order to assess sampling completeness by less subjective criteria, we compared observed species counts with predicted values obtained by nonparametric extrapolations.

The logic of extrapolating unobserved species richness from incomplete samples was recently reviewed by Colwell and Coddington (1994), and the application of certain nonparametric methods to our Paracou bat data was explained by Simmons and Voss (1998: 182–184). As in that study, we first consider the results of applying Chao's (1984) estimator, which is based on the total number of observed species, S_{obs}, the number of singletons (species recorded only once), a, and the number of doubletons (species recorded only twice), b. The expected total number of species, S^*, is then given by the expression

TABLE 53
Analysis of Sampling Completeness Using Chao's (1984) Species Richness Estimator for Methodologically Defined Partitions of the Paracou Nonvolant Mammal Inventory
(See text for explanation of symbols and computation.)

	S_{obs}	a	b	S^*	Confidence interval	Percent complete
Conventional trapping	18	2	4	19	17, 21	95
Arboreal trapping	6	2	2	7	4, 10	86
Pitfall trapping	12	6	2	21	6, 36	57
Diurnal hunting/census	16	5	2	22	10, 34	73
Nocturnal hunting/census	31	8	4	39	27, 51	79
Interviews	33	5	2	39	27, 51	85
ALL METHODS	64	8	4	72	60, 84	89

$$S^* = S_{obs} + (a^2/2b).$$

We constructed approximate 95% confidence intervals (±2 SD) using a formula for the variance given by Colwell and Coddington (1994) on the assumption that S^* is normally distributed (after Chao, 1987), and we estimated completeness as the percentage (S_{obs}/S^*) × 100.

The results of such calculations (table 53) suggest that sampling by some inventory methods was indeed more complete than sampling by others, although confidence intervals are wide enough to include the observed number of species in every case. Of particular interest is the apparent near-completeness of conventional trapping on the one hand, and the relative incompleteness of pitfall trapping on the other, estimates that more-or-less coincide with our subjective interpretation of species accumulation graphs. On the other hand, the rather high completeness estimate for arboreal trapping is difficult to reconcile with our scant capture success using this method.

Given the inherent uncertainty of all extrapolation procedures, other estimates of S^* are of interest in order to bracket the range of plausible inferences that can be based on our sampling data. We therefore used three additional nonparametric species-richness estimators to assess inventory completeness (table 54). By each estimator, our conventional-trapping data appear to be the most complete (although not always by a large margin), and our pitfall-trapping data the least complete. The remaining data partitions (arboreal trapping, diurnal hunting, nocturnal hunting, interviews) are not consistently ranked inter se by completeness. Perhaps the best synthesis of these results is obtained by taking average completeness values across all four sets of extrapolation figures, which yields the sequence: conventional trapping > arboreal trapping and interviews > nocturnal hunting > diurnal hunting > pitfall trapping.

Pooling sampling results from all nonvolant inventory methods, eight species are each represented in our data by single records (*Gracilinanus emiliae, Cabassous unicinctus, Saimiri sciureus, Galictis vittata, Neacomys dubosti, Coendou melanurus, Makalata didelphoides, Mesomys* sp.) and four species are represented by just two records each (*Priodontes maximus, Cyclopes didactylus, Nectomys melanius, Neusticomys oyapocki*). Using Chao's (1984) extrapolation procedure (table 53), the predicted total nonvolant species richness at Paracou is 72 species, an estimate that suggests our nonvolant inventory is 89% complete. Other nonparametric estimators yield S^* values in the range of 69–74 species and corresponding completeness estimates of 86–93% (table 54).

Obviously, neither the presence of additional nonvolant species in the Paracou fauna nor their absence can be proven without additional fieldwork. However, it is noteworthy that the numbers of missing species implied by these statistical extrapolations (5–10, calculated as S^* minus S_{obs}) correspond closely with the number of additional species that

TABLE 54
Analyses of Sampling Completeness Using Alternative Species Richness Estimators[a]

	CHAO2		JACK1		JACK2	
	S^*	% complete	S^*	% complete	S^*	% complete
Conventional trapping	19	95	20	90	18	100
Arboreal trapping	7	86	8	75	7	86
Pitfall trapping	37	32	19	63	25	48
Diurnal hunting/census	22	73	21	76	24	67
Nocturnal hunting/census	37	84	39	79	42	74
Interviews	39	85	38	87	41	80
ALL METHODS	69	93	72	89	74	86

[a] Abbreviations: CHAO2, the method described by Chao (1984) as modified for analyzing presence-absence among samples by Colwell and Coddington (1994); JACK1, the first-order jackknife (Burnham and Overton, 1979; Heltshe and Forrester, 1983); JACK2, the second-order jackknife (Burnham and Overton, 1979). All of these methods are based on species representation by sampling date, not individual records (see Colwell and Coddington, 1994). The number of "unicates" (species recorded on just one sampling date) and the number of "duplicates" (species recorded on just two dates) in our data are (2, 4) for conventional trapping, (2, 3) for arboreal trapping, (7, 1) for pitfall trapping, (5, 2) for diurnal hunting, (8, 5) for nocturnal hunting, (5, 2) for second-hand observations (from interviews), and (8, 6) for the pooled results of all methods. The algebra of CHAO2 is the same as that for Chao's (1984) method (with unicates substituted for singletons and duplicates for doubletons; see text), but the jackknife methods require counts of sampling dates (t) to compute the multipliers a_{ik} for the ith frequency class of the kth-order richness estimator (Burnham and Overton, 1979). We used the following counts for calculating S^* with JACK1 and JACK2: conventional trapping, $t = 79$ dates; arboreal trapping, 47; pitfall trapping, 54; diurnal hunting, 202; nocturnal hunting, 123. The number of sampling dates effectively represented by our interview results and by ALL METHODS (which includes interview data) is unknown but must be very large; for these data we used the limiting values for the a_{ik} suggested by Burnham and Overton (1979: 935).

could be expected to occur locally on the basis of known geographic and ecological distributions (appendix 1). Presumably, that short list (*Didelphis albiventris, Marmosa lepida, Cebus olivaceus, Leopardus tigrinus, Oecomys bicolor, Oecomys rex, Rhipidomys leucodactylus, Echimys chrysurus, Isothrix sinnamariensis*) includes the likeliest candidates for discovery by future inventory efforts at Paracou.

DISCUSSION OF THE NONVOLANT FAUNA

Although a few nonvolant species were always common and easily observed at Paracou, most were uncommon or cryptic. Our sampling data are therefore much sparser for nonvolant mammals (583 records total, summed over all methods excluding interviews) than for bats (3126 records; Simmons and Voss, 1998). Furthermore, because most protocols for sampling nonvolant mammal diversity were very labor-intensive, available effort had to be allocated among just a few methods in each field season; as a result, none were applied continuously or with comparable intensity throughout our study. Finally, the same labor constraints dictated that most of our nonvolant mammal sampling was restricted to primary forest with only minimal coverage of secondary vegetation.

As a consequence of these limitations, we cannot provide the same detail of analysis for nonvolant mammal sampling that we were previously able to accomplish with our bat data. For example, available nonvolant mammal records from Paracou are simply too sparse, too spatiotemporally biased, and/or too methodologically heterogeneous to validly compare the faunas of different local habitats, or to compare rates of species accumulation in different field seasons. Additionally, the obvious effects of hunting on local game populations (see Primates, above), together with the dramatic decline in abundance of small rodents and marsupials after 1991 (see results for Conventional Trapping, above), suggest that we were not effectively sampling the same nonvolant fauna throughout the course of our project. The data at hand are therefore less than ideal for testing ecological or methodological hypotheses.

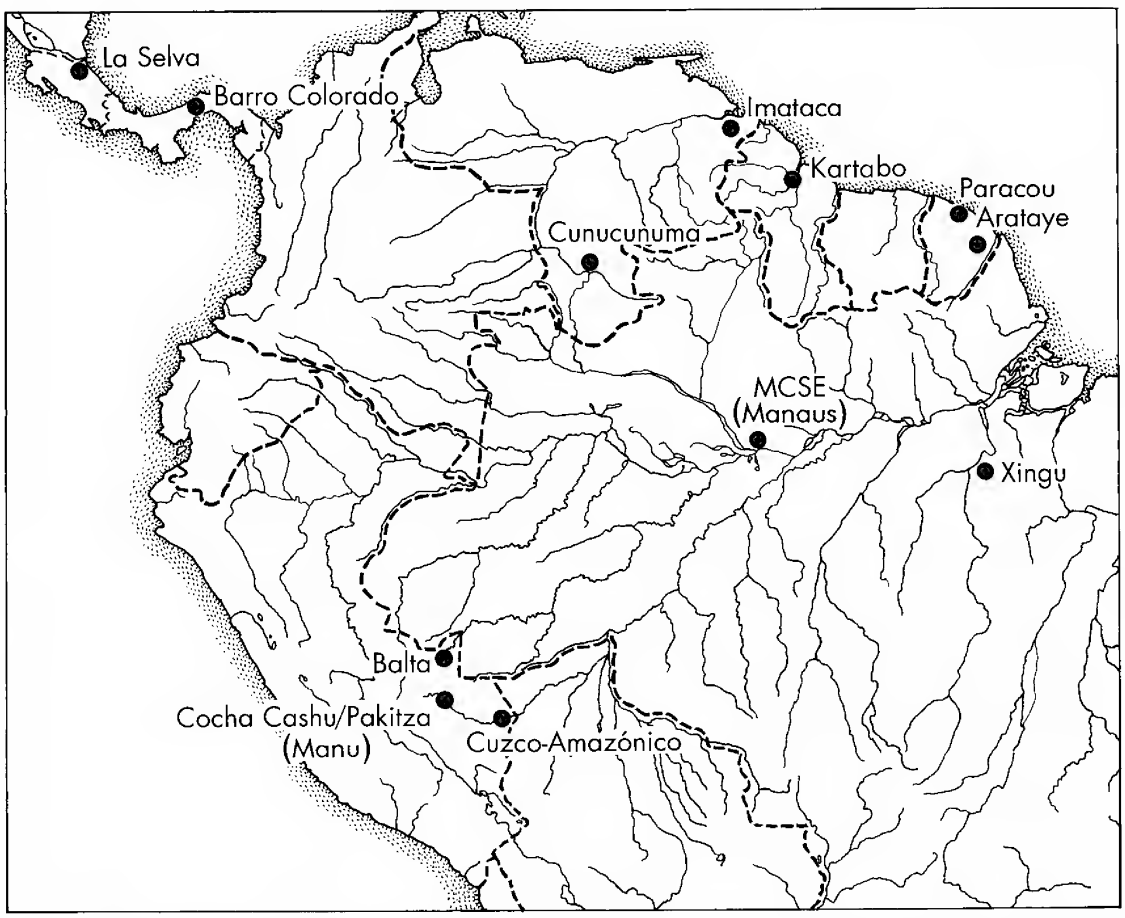

Fig. 88. Twelve Neotropical rainforest localities from which nonvolant mammal diversity data were compiled for this report. See footnotes to table 55 for geographic coordinates and references.

Nevertheless, nonparametric species-richness estimators applied to the pooled results of all methods (including interviews) suggest that our nonvolant inventory is about 90% complete, and it therefore seems unlikely that faunistic inferences—about taxonomic composition, zoogeographic relationships, species richness, etc.—will be substantially altered by future fieldwork at Paracou. In order to provide a comparative context for discussing such topics, we surveyed the literature and identified 11 other Neotropical rainforest sites, 2 in Central America and 9 in Amazonia, from which large species lists of nonvolant mammals have been published. These localities are mapped in figure 88, the taxonomic distribution of nonvolant species richness at each site is summarized in table 55, and a complete species-by-locality matrix is provided in appendix 2.

Taxonomic Composition and Biogeography

In terms of higher-level taxonomic composition, the nonvolant mammals of Paracou represent a typical Neotropical lowland rainforest fauna. Seven of the eight orders commonly found in Central and South American rainforests (Marsupialia, Xenarthra, Primates, Carnivora, Perissodactyla, Artiodactyla, Rodentia) are represented in our inventory; only Lagomorpha, which is never represented by more than a single species at any rainforest site, is absent. All of the families and genera of nonvolant mammals in the Par-

TABLE 55

Taxonomic Distribution of Nonvolant Mammalian Species Richness in 12 Neotropical Rainforest Faunas

(Table entries are numbers of species present.)

	Taxa[a]								
	Mar	Xen	Pri	Car	Per	Art	Rod	Lag	Total
Central America									
La Selva[b]	5	7	4	14	1	4	16	1	52
Barro Colorado[c]	6	6	4	13	1	4	14	1	49
Amazonia									
Imataca[d]	7	8	3	12	1	3	17	1	52
Kartabo[e]	7	9	6	13	1	4	20	0	60
Paracou	**12**	**9**	**6**	**10**	**1**	**4**	**22**	**0**	**64**
Arataye[f]	11	8	7	13	1	4	24	0	68
Cunucunuma[g]	8	7	7	7	1	2	12	0	44
MCSE Reserves[h]	9	8	6	8	1	4	17	0	57
Xingu[i]	8	4	7	2	1	2	23	1	48
Balta[j]	11	9	10	15	1	3	24	1	74
Manu[k]	12	7	13	14	1	4	27	1	79
Cuzco Amazónico[l]	9	5	7	11	1	3	22	1	59

[a] Excluding Cetacea and Sirenia. Abbreviations: Mar, Marsupialia; Xen, Xenarthra; Pri, Primates; Car, Carnivora; Per, Perissodactyla; Art, Artiodactyla; Rod, Rodentia; Lag, Lagomorpha.

[b] La Selva (10°26′N, 83°59′W) is a research station in the Caribbean lowlands of Heredia province, Costa Rica (Voss and Emmons, 1996: appendix 2).

[c] Barro Colorado Island (9°09′N, 79°51′W) is a research station in the former Canal Zone of central Panama (Voss and Emmons, 1996: appendix 3).

[d] The Reserva Forestal de Imataca straddles the Venezuelan states of Delta Amacuro and Bolívar (Ochoa, 1995); the species counts tabulated here are from "Unidad V," Ochoa's (1995) principal inventory area, centered at ca. 7°45′N, 61°10′W. This list excludes several nonforest mammals collected or observed in Unidad V (*Cerdocyon thous, Odocoileus cariacou, Zygodontomys brevicauda*), one murid that we judged to be unidentifiable without voucher material (*Oecomys "concolor"*), and one echimyid of uncertain identification (*Proechimys* sp.).

[e] Kartabo (6°23′N, 58°41′W) is a former research station of the New York Zoological Society at the confluence of the Cuyuni and Mazaruni rivers, Mazaruni-Potaro District, Guyana (Voss and Emmons, 1996: appendix 4).

[f] We combine inventory data from adjacent research stations of the Muséum National d'Histoire Naturelle, Les Nouragues (4°05′N, 52°40′W) and Saut Pararé (4°02′N, 52°42′W), both of which are in the lower Arataye catchment of east-central French Guiana (Voss and Emmons, 1996: appendix 5). The species counts tabulated here include two marsupials (*Didelphis albiventris, Marmosa lepida*), two carnivores (*Pteronura brasiliensis, Leopardus tigrinus*), and three rodents (*Oecomys bicolor, Oecomys rutilus, Rhipidomys nitela*) previously unknown from this fauna (new records courtesy of F. Catzeflis and P. Charles-Dominique, personal commun.).

[g] We combine inventory data from Culebra (3°39′N, 65°46′W) and Acanaña (3°32′N, 65°48′W), two Yekuana villages on the Río Cunucunuma in the Venezuelan federal territory of Amazonas (Voss and Emmons, 1996: appendix 6). Included in the species counts tabulated here is a previously unreported record of *Neacomys* sp. (voucher in USNM).

[h] The Minimum Critical Size of Ecosystems reserves (ca. 2°30′S, 60°W) are located about 80 km N Manaus in the Brazilian state of Amazonas (Voss and Emmons, 1996: appendix 7).

[i] A Smithsonian collecting locality on the right (east) bank of the Rio Xingu (at 3°39′S, 52°22′W) in the Brazilian state of Pará (Voss and Emmons, 1996: appendix 8).

[j] Balta (10°08′S, 71°13′W) is a Cashinahua village on the Río Curanja in the Peruvian department of Ucayali (Voss and Emmons, 1996: appendix 9).

[k] We combine inventory data from Cocha Cashu (11°54′S, 71°22′W) and Pakitza (11°57′S, 71°17°W), adjacent inventory sites on the left (north) bank of the Río Manu in the Peruvian department of Madre de Dios (Voss and Emmons, 1996: appendix 10).

[l] Cuzco Amazónico (12°33′S, 69°03′W) is an ecotourist lodge on the left (north) bank of the Río Madre de Dios in the Peruvian department of Madre de Dios (Voss and Emmons, 1996: appendix 11).

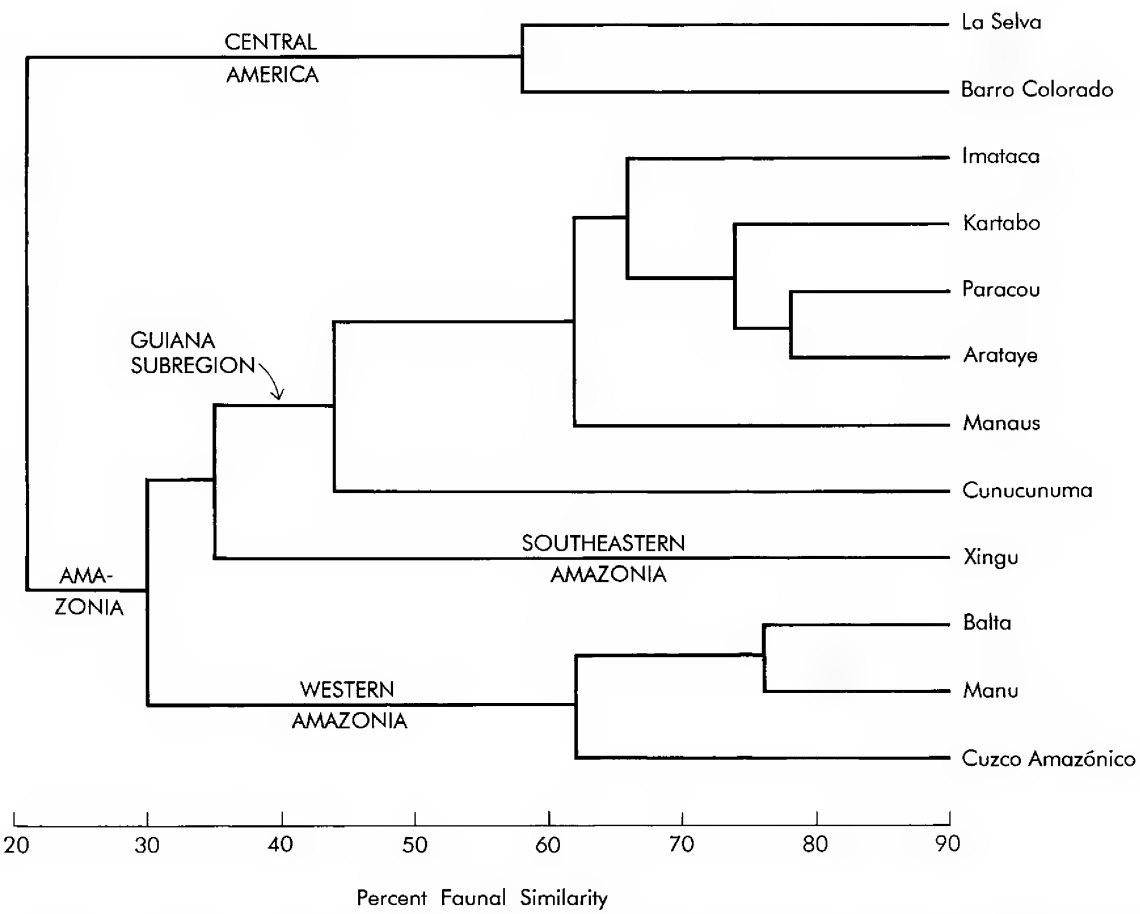

Fig. 89. Analysis of faunal similarity among nonvolant mammal inventories from 12 Neotropical rainforest localities. Faunal similarity was quantified between each pair of localities (*i, j*) by Jaccard's coefficient, $J_{ij} = C_{ij}/T_{ij}$, where C_{ij} is the number of species common to both faunas and T_{ij} is the total number of species in both faunas combined ($T_{ij} = N_i + N_j - C_{ij}$). Localities were clustered by the unweighted pair-group method using arithmetic averages (Sneath and Sokal, 1973) for comparability with other recent biogeographic analyses of Neotropical vertebrates (e.g., da Silva and Sites, 1995). The bottom scale shows the clustering level in units of percent faunal similarity ($J \times 100$). No historical or other causal interpretation is implied by these results, nor do we assume that a hierarchical model is necessarily appropriate except as a convenient summary graphic.

acou fauna are likewise widespread rainforest taxa.

In terms of species composition, Paracou clusters (fig. 89) with five other faunas from the Guiana subregion of Amazonia, next with a single southeastern Amazonian site, then with a discrete grouping of three western Amazonian localities, and lastly with a pair of Central American faunas. Pairwise measures of faunal resemblance (table 56) indicate that the Paracou nonvolant inventory is most similar to that from Arataye, another French Guianan locality only 136 km to the SSE, and least similar to that from La Selva, a Costa Rican locality almost 3400 km to the WNW. Overall, these results clearly indicate a pattern of increasing faunal resemblance with increasing geographic proximity, and that the Paracou fauna in particular is most similar to others from northeastern Amazonia.

Paracou nonvolant mammals can be sorted (table 57) into seven groups based on their pattern of distribution among the four Neo-

TABLE 56
Percent Similarity Among Nonvolant Mammal Faunas from 12 Neotropical Rainforest Inventory Sites[a]
(Table entries are Jaccard's coefficient[b] × 100.)

Bco	58										
Ima	21	25									
Kar	19	24	67								
Par	**20**	**21**	**61**	**72**							
Ara	20	23	69	75	**78**						
Cun	17	18	43	42	**41**	46					
Man	17	19	57	59	**64**	68	47				
Xin	10	16	33	33	**36**	38	28	42			
Bal	24	28	37	35	**36**	38	30	32	22		
CCP	21	26	31	30	**29**	32	26	29	22	76	
CAm	24	24	31	27	**29**	31	26	29	23	65	63
	LSe	BCo	Ima	Kar	**Par**	Ara	Cun	Man	Xin	Bal	CCP

[a] Abbreviations: LSe, La Selva (Costa Rica); BCo, Barro Colorado (Panama); Ima, Imataca (Venezuela); Kar, Kartabo (Guyana); Par, Paracou (French Guiana); Ara, Arataye (French Guiana); Cun, Cunucununa (Venezuela); Man, Manaus (= MCSE reserves, Brazil); Xin, Xingu (Brazil); Bal, Balta (Peru); CCP, Cocha Cashu/Pakitza (= Manu, Peru); CAm, Cuzco Amazónico (Peru). See footnotes to table 55 for geographic information and references.

[b] The calculation of Jaccard's coefficient is explained in the caption to figure 89, and the raw (presence/absence) data are provided in appendix 2. Note that incomplete sampling generally underestimates biotic similarity, for the same reasons that complementarity is generally overestimated by incomplete samples (Colwell and Coddington, 1994). Because complementarity can be expressed as the one-complement of Jaccard's coefficient (op. cit.), the values in this table can be subtracted from 100 to obtain percent complementarity (the fraction of the combined fauna from two sites that is not shared between them).

tropical lowland rainforest regions recognized by Voss and Emmons (1996). The largest distributional group (pattern 1) includes 24 species that are endemic to Amazonia (A), or are even more narrowly restricted to the Guianan (G) subregion of Amazonia: *Hyladelphys kalinowskii* (A), *Marmosops parvidens* (A), *Marmosops pinheiroi* (A), *Monodelphis brevicaudata* (G), *Dasypus kappleri* (A), *Saguinus midas* (G), *Ateles paniscus* (G), *Pithecia pithecia* (G), *Saimiri sciureus* (A), *Sciurillus pusillus* (A), *Sciurus aestuans* (G), *Neacomys dubosti* (G), *Neacomys paracou* (G), *Neusticomys oyapocki* (G), *Oecomys auyantepui* (G), *Oecomys rutilus* (G), *Oryzomys macconnelli* (A), *Oryzomys yunganus* (A), *Rhipidomys nitela* (A), *Coendou melanurus* (G), *Myoprocta acouchy* (A), *Mesomys* sp. (G), *Proechimys cuvieri* (A), and *Proechimys guyannensis* (A). Therefore, a substantial fraction (38%) of the Paracou fauna is distinctively Amazonian or Guianan in character.

TABLE 57
Rainforest Distribution Patterns of Nonvolant Paracou Mammals

Pattern	Rainforest distribution[a]				No. of species
	trAnd	CoVen	Ama	Atl	
1			X		24
2	X	X	X	X	18
3		X	X		9
4		X	X	X	7
5	X	X	X		4
6	X		X	X	1
7			X	X	1

[a] Abbreviations of Neotropical lowland rainforest regions as defined by Voss and Emmons (1996): trAnd, trans-Andean (including Central America and the Chocó); CoVen, Coastal Venezuelan; Ama, Amazonian; Atl, Atlantic (southeastern Brazil).

The next-largest distributional group (pattern 2) includes 18 species that (as currently recognized by taxonomists) occur in all four Neotropical rainforest regions. These essentially pan-Neotropical taxa include *Chironectes minimus, Metachirus nudicaudatus, Dasypus novemcinctus, Myrmecophaga tridactyla, Speothos venaticus, Herpailurus yagouarondi, Leopardus pardalis, Leopardus wiedii, Panthera onca, Puma concolor, Eira*

barbara, Galictis vittata, Potos flavus, Mazama americana, Mazama gouazoubira, Pecari tajacu, Tayassu pecari, and *Cuniculus paca.* Pending future revisionary study (see below), this group of species, comprising about 28% of the fauna, is zoogeographically uninformative.

By contrast, other Paracou nonvolant mammals are neither Amazonian endemics (as currently recognized) nor pan-Neotropical, but have distributions that suggest a variety of inter-regional connections. Thus, nine species occur in both Amazonian and Coastal Venezuelan rainforests, but not in the other two regions (pattern 3: *Gracilinanus emiliae, Bradypus tridactylus, Choloepus didactylus, Cabassous unicinctus, Priodontes maximus, Alouatta seniculus, Nectomys melanius, Oryzomys megacephalus, Makalata didelphoides*), seven species occur in all rainforest regions except the trans-Andean (pattern 4: *Caluromys philander, Marmosa murina, Micoureus demerarae, Tamandua tetradactyla, Tapirus terrestris, Coendou prehensilis, Dasyprocta leporina*), and four species occur in all rainforests except the Atlantic region of southeastern Brazil (pattern 5: *Didelphis marsupialis, Philander opossum, Cyclopes didactylus, Oligoryzomys fulvescens*). One species (*Nasua nasua*) occurs in all rainforest regions except the Coastal Venezuelan (pattern 6), and another (*Cebus apella*) occurs only in Amazonia and the Atlantic rainforest region of southeastern Brazil (pattern 7).[25]

Of course, not all of the nonvolant species that belong to the Paracou fauna are restricted to rainforest habitats: many are eurytopic and occur in a wide range of other Neotropical biomes. For example, at least 16 of the 18 species with distributional pattern 2 are also known from the Llanos (Eisenberg et al., 1979; Ibáñez, 1981), the Caatinga (Willig and Mares, 1989), the Cerrado (Redford, 1983; Fonseca and Redford, 1984; Mares et al., 1989), or the Pantanal (Schaller, 1983). On the other hand, none of the taxa that we recorded at Paracou are consistently associated elsewhere with nonforest habitats. A few Paracou species (*Marmosa murina, Saimiri sciureus, Oligoryzomys fulvescens*) are perhaps never found in unbroken tracts of Guianan rainforest, but these can be characterized as inhabitants of the rainforest edge that probably occur along riverbanks, blowdowns, and other natural openings at undisturbed sites. Several unambiguously nonforest mammals might inhabit the coastal savannas and salt marshes just north of our study area (e.g., *Odocoileus cariacou, Holochilus sciureus, Zygodontomys brevicauda*), but none were encountered within our sampling radius. Therefore, although some nonvolant Paracou mammals are not rainforest specialists, the fauna as a whole includes only species that are known to occur in rainforested landscapes and appears to constitute an ecologically homogeneous assemblage.

Species Richness

Comparisons of nonvolant mammal species richness among Neotropical rainforest inventories are complicated by many factors. As documented in the preceding analyses of sampling results, different inventory methods effectively sample different sets of species, and increased effort with any method generally produces more species. Therefore, even in the absence of real intersite diversity differences, long-term inventories (or those using more methods) would be expected to obtain larger species lists than short-term inventories (or those using fewer methods). Differences in the ecological scope of inventory fieldwork can also affect species richness comparisons because sites with greater habitat diversity will tend to be richer than sites with fewer habitats. Finally, large mammals are likely to be more abundant, and

[25] Because so few genera of nonvolant mammals in the Paracou fauna have been revised, it is prudent to consider how the memberships of these distributional groups are likely to change with future taxonomic research. In fact, morphological and/or molecular data are already available to suggest that many widely distributed nonvolant "species" are composite (i.e., consist of two or more diagnosable geographic forms that should be recognized as valid taxa; see Remarks above for *Caluromys philander, Marmosa murina, Metachirus nudicaudatus, Micoureus demerarae, Philander opossum,* and *Mazama gouazoubira*). Although it is also possible that a few species currently thought to be Amazonian endemics will eventually be found to occur in other rainforest regions, the likely net outcome of future research will be to decrease significantly the number of valid species with widespread distributions and to increase the number of species with more restricted ranges.

TABLE 58
Methodological Comparisons among Nonvolant Mammal Inventories from Three Neotropical Rainforest Localities

	Years	Prior defaunation?	Methods[a]						Source
			CT	AT	PT	DH	NH	IN	
La Selva	34	no	X			X	X		Voss and Emmons (1996: appendix 2)
Paracou	4	some	X	X	X	X	X	X	This report
Manu	21	no	X	X		X	X		Voss and Emmons (1996: appendix 10)

[a] Abbreviations: CT, conventional trapping; AT, arboreal trapping; PT, pitfall trapping; DH, diurnal hunting; NH, nocturnal hunting; IN, interviews.

therefore more easily recorded, at undisturbed localities than at sites which have been partially defaunated by hunting.

Published descriptions of inventory fieldwork (cited in the footnotes to table 55) document intersite differences in all of these potentially confounding factors: (1) Although fieldworkers at all sites used conventional trapping, diurnal hunting, and nocturnal hunting to sample nonvolant mammal diversity, other methods (pitfall trapping, arboreal trapping, and interviews) were less consistently applied, and no previous inventory has used all six methods in combination. (2) Overall sampling effort is hard to quantify for nonvolant mammal surveys, but the duration of inventory work at each site (a monotonic correlate of effort) ranged from less than a year at some sites to many years at others. (3) Whereas most sites were located on rivers or lakes that provide habitat for semiaquatic, riparian, and forest-edge species, others were in well-drained uplands remote from large bodies of water. (4) Subsistence hunting probably eliminated some primates and other large species prior to inventory fieldwork at several sites, whereas other sites were pristine.

As a consequence of such disparities, tabulated species counts are undoubtedly affected by sampling artifacts to a greater or lesser extent. The most that can be said from these data, without introducing additional assumptions or corrections, is that nonvolant species richness at Paracou more nearly resembles that from other well-sampled sites in the Guiana subregion of Amazonia (e.g., Kartabo, Arataye) than they do Central American sites (which have fewer species for most orders) or western Amazonian sites (which tend to have more species). To better exemplify regional and subregional differences in species richness, we focus our comparisons on two sites where prolonged fieldwork may have compensated in some degree for methodological incompleteness (table 58).

La Selva (with over 30 years of faunal observations) probably provides the best-sampled nonvolant mammal fauna from any Central American lowland rainforest, and Manu (with over 20 years) provides an appropriate western Amazonian counterpart. Although it is not possible to estimate sampling completeness at either of these sites by extrapolation (requisite frequency data are not available), surrogate estimates can be based on the number of rainforest species expected at each locality from geographic range data. Such calculations (see Voss and Emmons, 1996: table 10) suggest that the La Selva nonvolant inventory is about 95% complete and the Manu nonvolant inventory about 85% complete. By any of the extrapolations computed earlier in this report, the Paracou nonvolant fauna falls between La Selva and Manu in estimated completeness (86–93%). Therefore, known species richness and estimated completeness are inversely correlated among these three inventories.

Graphical comparisons (fig. 90) summarize the principal higher-taxonomic patterns of species richness among La Selva, Paracou, and Manu. Intersite differences in known species richness are most pronounced for Marsupialia, Primates, and Glires (Rodentia + Lagomorpha). For each of these clades, La Selva is the least diverse site; Paracou and Manu are equivalent in known marsupial diversity, but Manu is more diverse than Paracou for both primates and rodents. Paracou

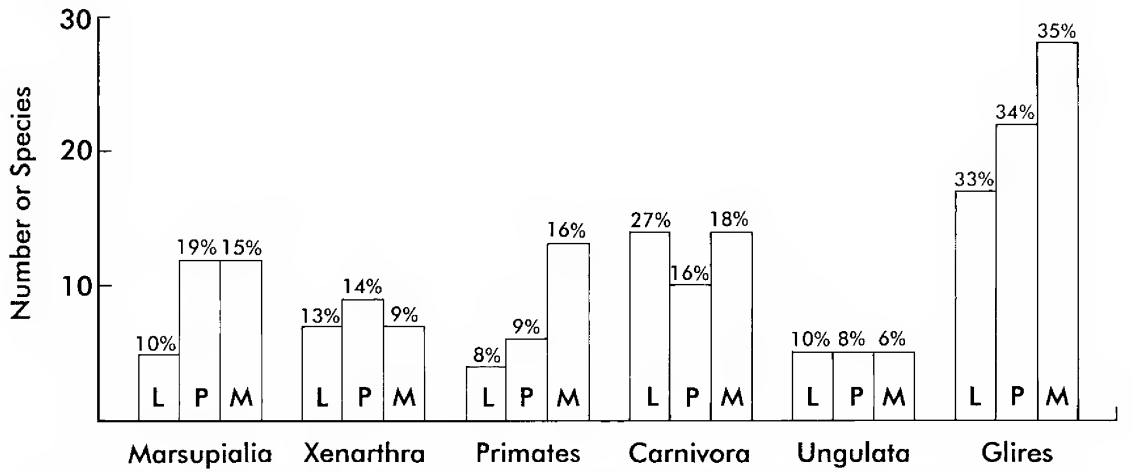

Fig. 90. Species richness comparisons for higher-level clades at three Neotropical rainforest sites. For each clade, bar height indicates the number of species at La Selva (**L**), Paracou (**P**), and Manu (**M**); percentages above each bar indicate the relative contribution of those species to the entire nonvolant fauna at each site. Artiodactyla and Perissodactyla are combined as Ungulata, Rodentia and Lagomorpha as Glires.

has the most known xenarthran species of any site, but the least number of known carnivore species; ungulate species richness is invariant. Overall, known nonvolant species richness increases by 12 from La Selva to Paracou, and by 15 from Paracou to Manu; from La Selva to Manu, the net increase in species richness (27 species) amounts to 52% of the former fauna. Given the previously noted inverse correlation between known species richness and estimated inventory completeness, the true diversity gradient from La Selva to Paracou to Manu is likely to be even steeper than these quantities imply.

Whereas Glires is the most diverse clade at each locality (accounting for an almost constant proportion, 33–35%, of the local nonvolant species), the remaining clades are not consistently ranked by species richness. At La Selva, Carnivora is the most speciose after Glires, distantly followed by Xenarthra; Marsupialia and Ungulata are next, and Primates is last. At Paracou, however, Marsupialia is more speciose than Carnivora, which is closely followed by Xenarthra; Primates is next, followed by Ungulata. At Manu, Carnivora is again the most speciose clade after Glires, but Primates is almost as diverse, followed closely by Marsupialia; Xenarthra is next and Ungulata is last.

Although some of these faunal differences are probably artifactual,[26] the short lists of expected species for each locality (Voss and Emmons, 1996: appendices 2, 10; this report: appendix 1) suggest that future inventory work is unlikely to change the overall picture very much. For example, primates are likely to remain in last place at La Selva, as are ungulates at Paracou and Manu. A few clades may switch ranks at some sites (e.g., marsupials may prove to be more diverse than primates at Manu), but the larger diversity differences (among clades at each locality, and among localities for the same clade) are probably robust.

Clearly, exemplar comparisons can be over-interpreted, and it would be unwise to make sweeping generalizations about geographic diversity patterns based on just these three sites. Nevertheless, the nonvolant mammal fauna at Paracou is probably represen-

[26] Three uncontrolled factors seem most likely to have affected our faunal comparisons, First, bodies of water suitable for otters and other large semiaquatic or riparian mammals are present at La Selva and Manu, but not at Paracou. Second, the long duration of inventory work at La Selva and Manu has probably been insufficient to fully compensate for the lack of methods suitable for detecting all of the small and elusive nonvolant species at those sites. Third, interviews at Paracou may not have compensated fully for the partial defaunation of our study area prior to this inventory.

tative of that throughout most of the Guiana subregion of Amazonia, which would appear to be richer in species (especially of marsupials and rodents) than Central American rainforest faunas, but less species-rich (especially in primates) than western Amazonian faunas. Although such regional and subregional diversity contrasts could have historical explanations, it is nevertheless appropriate to explore their consequences for the ecological structure of contemporary communities, which may suggest other causal factors.

Trophic Guilds and Other Topics

Several previous studies have tabulated the ecobehavioral attributes of nonvolant rainforest mammals at various Neotropical inventory sites (e.g., Eisenberg and Thorington, 1973; Janson and Emmons, 1990; Peres, 1999), but none have provided a comprehensive trophic classification. Indeed, there are many problems in attempting to do so. Whereas most rainforest bats can be sorted into guilds based on reasonably straightforward dietary and behavioral attributes (Bonaccorso, 1979; Kalko et al., 1996; Simmons and Voss, 1998), many nonvolant mammals are harder to characterize ecologically. Numerous species feed on fruit when it is seasonally abundant, but switch to different resources when fruit is scarce; for example, woody browse (*Mazama americana*; Bodmer, 1990), seeds (*Dasyprocta leporina*; Henry, 1999), or animals (many didelphids; Atramentowicz, 1988). The poorly documented or completely unknown food habits of some nonvolant taxa (e.g., *Glironia, Sciurillus,* many murids) is another obstacle to trophic classification.

Foraging substrate is an important factor in defining nonvolant guilds that introduces additional ambiguities because many species do not restrict their activities to one substrate type. Whereas some taxa are unambiguously terrestrial or arboreal, numerous trapping and observational studies (e.g., Janson and Emmons, 1990; Malcolm, 1991; Woodman et al., 1995; this study) suggest that others are scansorial—active both in trees and on the ground. Similarly, whereas some species that forage primarily in water are unambiguously semiaquatic (*Chironectes, Lontra*), others forage at or near the water's edge (*Procyon, Nectomys, Hydrochoerus*) and are perhaps better described as riparian. Unfortunately, it is difficult to classify species by such subtle (but perhaps important) behavioral distinctions in the frequent absence of relevant field studies.

Despite these and other problems, some guilds of nonvolant rainforest mammals have been widely and more-or-less consistently recognized (e.g., arboreal folivores; Montgomery, 1978), and others can readily be defined to label obvious clusters of ecologically similar species (e.g., terrestrial granivore/frugivores; Peres, 1999). By adopting or modifying some previously recognized ecobehavioral categories and recognizing a few new ones, we were able to sort most of the nonvolant taxa from La Selva, Paracou, and Manu into a reasonably small number of guilds (table 59). Obviously, some of these are very broadly defined—such as terrestrial animalivores—and could be further subdivided for more detailed analyses. Alternatively, many could be combined for the purposes of broader generalizations (e.g., about primary versus secondary consumers). In effect, we tried to achieve a balance between excessively fine distinctions on the one hand and insufficient resolution on the other while minimizing the number of arbitrary decisions necessary to assign taxa to different categories.

We primarily used natural history data summarized by Emmons (1997) to assign taxa to guilds, but we consulted other references for supplementary information. When two or more references suggested different guild assignments for the same taxon, we based our final assignment on the most detailed available field study or the most thorough literature review. Unavoidably, many guild assignments are arguable (how much more fruit in the diet should distinguish a frugivore from an omnivore?), and some are frankly speculative (e.g., dietary categories for most murids). However, insofar as possible we used consistent criteria from locality to locality, so the results are hopefully unbiased for comparative purposes.

Arboreal Folivores: This guild is represented by just three species at Paracou, two

TABLE 59

Guild Composition of Nonvolant Mammal Faunas from Three Neotropical Rainforest Localities[a]

	La Selva	Paracou	Manu
Arboreal folivores[b]	3 (6%)	3 (5%)	4 (5%)
Arboreal frugivores[c]	6 (12%)	5 (8%)	13 (16%)
Arboreal granivore/frugivores[d]	6 (12%)	9 (14%)	10 (13%)
Arboreal gummivores[e]	0 (0%)	0 (0%)	1 (1%)
Arboreal omnivores[f]	3 (6%)	5 (8%)	5 (6%)
Arboreal insectivores[g]	2 (4%)	2 (3%)	2 (3%)
Arboreal unknowns[h]	0 (0%)	3 (5%)	2 (3%)
Terrestrial herbivores[i]	2 (2%)	0 (0%)	2 (3%)
Terrestrial granivore/frugivores[j]	11 (21%)	13 (20%)	14 (18%)
Terrestrial folivore/frugivores[k]	3 (6%)	3 (5%)	3 (4%)
Terrestrial omnivores[l]	2 (4%)	2 (3%)	2 (3%)
Terrestrial animalivores[m]	11 (21%)	16 (25%)	15 (19%)
Semiaquatic/riparian folivores[n]	0 (0%)	0 (0%)	1 (1%)
Semiaquatic/riparian omnivores[o]	0 (0%)	1 (2%)	1 (1%)
Semiaquatic/riparian animalivores[p]	3 (6%)	2 (3%)	4 (5%)

[a] Table entries are numbers of species in each fauna belonging to each guild, followed by the percentage of the total fauna that those species represent (in parentheses). The following conventions were followed in compiling these data: (1) arboreal guilds include scansorial species; (2) "omnivores" eat roughly equal proportions of plant and animal tissues (other trophic descriptors imply predominance of either plants or animals in known or inferred diets); (3) unstudied species are assignable to the same guild as congeners with known diets and behavior; (4) rodents are granivore/frugivores in the absence of compelling evidence to the contrary. Most guild assignments were based on natural history information summarized by Emmons (1997), but additional supporting references are cited below.

[b] *Bradypus, Choloepus, Alouatta,* and *Dactylomys*. The diets of *Choloepus* and *Alouatta* also include fruit.

[c] *Caluromys, Caluromysiops,* most primates (*Alouatta, Callimico, Pithecia,* and *Saguinus midas* are exceptions), *Potos* (see Kays, 1999), and *Bassaricyon*. The diets of many species in this guild also include nectar.

[d] *Pithecia* (see Peres, 1993b), most sciurids (*Sciurillus* is the only known exception), arboreal murids (conjectural; no rainforest species has been studied in any detail), erethizontids, arboreal echimyids. Erethizontids also eat leaves and bark and might better be classified as arboreal folivores; no rainforest species has been adequately studied in the field.

[e] Consumers of saps and gums: *Callithrix pygmaea* (also eats insects).

[f] *Didelphis, Marmosa, Micoureus, Philander, Callimico,* and *Saguinus midas* (see Pack et al., 1999). Some species in this guild are also active on the ground.

[g] *Cyclopes* and *Tamandua*. The latter is also active on the ground.

[h] *Glironia, Gracilinanus, Hyladelphys,* and *Sciurillus*.

[i] Consumers of plant nonreproductive tissues (roots, stems, and leaves): *Orthogeomys, Dinomys,* and *Sylvilagus*. The membership of *Dinomys* in this guild is based on inferences from craniodental morphology.

[j] Tayassuids, *Heteromys,* most nonarboreal murids (largely conjectural; *Neusticomys* and *Oxymycterus* are exceptions), *Cuniculus, Dasyprocta, Myoprocta, Hoplomys,* and *Proechimys*. All rainforest murids probably also eat insects; species of *Oryzomys* and *Proechimys* are also known to eat mycorrhizal fungi (Janos et al., 1995), which might be an important component of most terrestrial rodent diets.

[k] *Tapirus* and cervids.

[l] *Eira* and *Nasua*. The former also forages in trees; *Didelphis* and *Philander* are arguably better placed in this guild than with arboreal omnivores.

[m] *Marmosops* (see text), *Metachirus* (see text), *Monodelphis,* dasypodids, *Myrmecophaga,* canids, felids, *Conepatus, Galictis, Mustela,* and *Oxymycterus*.

[n] *Hydrochoerus*.

[o] *Nectomys*.

[p] *Chironectes, Lontra, Pteronura, Procyon,* and *Neusticomys*.

of which are diurnal (*Bradypus tridactylus* and *Alouatta seniculus*) and one nocturnal (*Choloepus didactylus*). The same number of arboreal folivores, belonging to the same genera, are present at most Neotropical rainforest sites except where a fourth taxon (*Dactylomys*) feeds in bamboo and other dense vegetation growing on rich alluvial soils (as at Manu; Emmons, 1997).

Although it is probable that howler populations had been depleted by hunting in our study area, it is unlikely that local sloth populations were significantly affected. For *Choloepus,* the only taxon for which intersite density comparisons are possible, our sighting rate by walked nocturnal census (0.08 individuals per 10 hours; table 51) is about one-eighth the rate reported by Emmons (1984)[27] at Limoncocha, a western Amazonian locality with rich soils, and one-fourth the average sighting rate on Barro Colorado Island (Glanz, 1982). Although our infrequent views of *Choloepus* and our inability to obtain even a single sighting of *Bradypus* suggest that sloths are locally rare, these taxa were among the commonest mammals rescued from primary forest flooded by a hydroelectric dam at Petit Saut, about 28 km SSW of our study area (Vié, 1999), where their joint density was estimated to be about 2.6 individuals/km^2 (Taube et al., 1999).

ARBOREAL FRUGIVORES: The most conspicuous intersite differences in trophic composition concern this guild, which contains only five species at Paracou, a mere 8% of the total nonvolant fauna. By contrast, six arboreal frugivores constitute 12% of the less speciose nonvolant fauna of La Selva, and 13 species constitute 16% of the more speciose fauna of Manu. The striking deficit of arboreal frugivores at Paracou is partly, but not entirely, a consequence of the previously noted faunal differences in primate diversity. Thus, although the Manu fauna includes several frugivorous primate genera not found at Paracou, it also includes additional nonprimate arboreal frugivores (*Caluromysiops, Bassaricyon*), one of which (*Bassaricyon*) also occurs at La Selva. Furthermore, whereas western Amazonian tamarins (members of the *Saguinus fuscicollis* and *S. mystax* groups, both of which occur at Manu) appear to be primarily frugivorous (Peres, 1993a), the single tamarin that occurs at Paracou, *S. midas,* is not (Pack et al., 1999). Because only one arboreal frugivore (*Cebus olivaceus*) is among the species that might have been locally extirpated by hunting prior to our inventory (or that might yet be discovered by future fieldwork; appendix 1), it seems unlikely that this guild is grossly underrepresented at Paracou as a consequence of sampling inadequacy.

All of the diurnal arboreal frugivores in our study area—*Ateles paniscus, Cebus apella, Saimiri sciureus*—were very uncommon, the first two probably as a consequence of persistent hunting. The only commonly encountered species belonging to this guild (*Caluromys philander, Potos flavus*) were both nocturnal. In fact, our sighting rate for kinkajous at Paracou (3.08 per 10 hours of walked nocturnal census) is comparable to the highest rate reported by Glanz (1982: table 4) from Barro Colorado Island, and is higher than any figures that Emmons (1984: table 4) reported from four Amazonian localities. This result seems anomalous in the context of other indications that the Paracou environment is not rich in fruit resources, but it is possible that kinkajous are locally abundant as a consequence of ecological release following the virtual extirpation of competing diurnal species. Our sighting rate for *Caluromys philander* (0.17 per 10 hours), however, is low by comparison with most reported rates for congeneric species on Barro Colorado Island (*C. derbianus*; Glanz, 1982: table 4) and in western Amazonia (*C. lanatus*; Emmons, 1984: table 4). It is noteworthy that trapping and sighting data for *C. philander* at Paracou are consistent with the results of other recent field studies (Charles-Dominique et al., 1981; Malcolm, 1991) in suggesting that this is one of the most exclusively arboreal of Amazonian marsupials.

ARBOREAL GRANIVORE/FRUGIVORES: This guild consists of nine species at Paracou, representing about 14% of the known nonvolant fauna. Roughly similar proportions of the La Selva and Manu faunas are arboreal grani-

[27] Emmons (1984) reported her census results as sightings per 10 km, and her walking speed as 0.6–1.5 km/hr. In comparing our results with hers, we assume that she walked about 1 km per hour on average.

vore/frugivores, despite geographic differences in taxonomic composition. Among other contrasts, Central American faunas contain no granivorous monkeys, whereas squirrels are more speciose in both Central America and western Amazonia than they are in the Guiana subregion.

Members of this guild at Paracou include two diurnal species, one a primate (*Pithecia pithecia*) and the other a squirrel (*Sciurus aestuans*); the remainder, three murids (*Oecomys auyantepui, O. rutilus, Rhipidomys nitela*) and four caviomorphs (*Coendou melanurus, C. prehensilis, Makalata didelphoides, Mesomys* sp.), are all nocturnal. All of the members of this guild except *Sciurus aestuans* and the murids were very uncommon at Paracou. Most of our scant field observations for these taxa are more-or-less consistent with previously published natural history data (summarized by Emmons, 1997), but the diurnal sighting of *Makalata didelphoides* is an inexplicable oddity.

ARBOREAL GUMMIVORES: No mammal in the Guiana subregion of Amazonia is known to subsist primarily on saps and gums, although it is possible that the unknown diet of *Sciurillus pusillus* includes some type of plant exudate (Emmons, 1997).

ARBOREAL OMNIVORES: Five Paracou species are assigned to this guild, constituting 8% of the known fauna. Proportions of arboreal omnivores in the La Selva and Manu faunas are similar.

At Paracou, arboreal omnivores consist of a single diurnal primate (*Saguinus midas*) and at least four nocturnal marsupials (*Didelphis marsupialis, Marmosa murina, Micoureus demerarae, Philander opossum*). Of the marsupials, our data suggest that *Micoureus* is the most consistently arboreal, followed by *Didelphis* and *Philander*; Paracou records are too scanty to place *Marmosa murina* in this ranking, but Charles-Dominique et al. (1981) suggested that this species is primarily active in the forest understory, like *P. opossum.* Most members of this guild were common in our study area, although numbers of *D. marsupialis* declined abruptly after 1991; only *M. murina* was consistently uncommon. Our nocturnal sighting rate for *P. opossum* (0.96 per 10 hours) is comparable to the highest rate reported for this species from Barro Colorado Island (Glanz, 1982: table 4) and is higher than either of the two previously reported rates from Amazonian localities (Emmons, 1984: table 4).

ARBOREAL INSECTIVORES: This guild includes only two species at Paracou and at all other adequately sampled Neotropical rainforest localities. Our field data contribute no new natural history information about either *Cyclopes* or *Tamandua.*

TERRESTRIAL HERBIVORES: The Paracou fauna includes no species assignable to this guild, nor (apparently) does any other known rainforest fauna from the Guiana subregion of Amazonia.

TERRESTRIAL GRANIVORE/FRUGIVORES: Thirteen species belong to this guild at Paracou, where they constitute 20% of the nonvolant fauna. Similar proportions of terrestrial granivore/frugivores are present in the La Selva and Manu faunas despite differences in the taxonomic composition of this group from site to site.

At Paracou, terrestrial granivore/frugivores include four large diurnal species (*Pecari tajacu, Tayassu pecari, Dasyprocta leporina, Myoprocta acouchy*), one large nocturnal species (*Cuniculus paca*), and eight small nocturnal species (*Neacomys dubosti, N. paracou, Oligoryzomys fulvescens, Oryzomys macconnelli, O. megacephalus, O. yunganus, Proechimys cuvieri, P. guyannensis*). Both of the peccaries, locally hunted for meat, were uncommon or wary; only *Dasyprocta* and *Myoprocta* were regularly seen (or heard) by us, but neither was really common. By contrast, our sighting rate for pacas (1.1 individuals per 10 hours of walked nocturnal census) is about equal to the average sighting rate (1.3 per 10 hours) for five Amazonian inventories tabulated by Emmons (1984: table 4), and is similar to sighting rates from two of the three nocturnal census episodes recorded for Barro Colorado Island (Glanz, 1982: table 4). It is possible that pacas are relatively common at Paracou for the same reason that kinkajous are, because local populations of most competing species in the diurnal fauna have been depleted by hunting.

Small nocturnal members of this guild accounted for 68% of our captures using all conventional traps, and 80% of our captures using just Victor and Sherman traps. Inter-

estingly, this is the only guild at Paracou where sympatry between congeneric forms is the rule rather than the exception: *Neacomys, Oryzomys,* and *Proechimys* are each represented by two or more species in the local fauna. Although most of the small nocturnal granivore/frugivores we recorded at Paracou occur syntopically in well-drained primary forest (the only exception is *Oligoryzomys fulvescens,* found exclusively in roadside secondary growth), our capture results suggest that some closely related species may differ in their use of other habitats. Thus, *Oryzomys yunganus* occurs more frequently than *O. megacephalus* in swampy and creekside forest, whereas *Proechimys cuvieri* occurs more frequently than *P. guyannensis* in secondary growth. To the best of our knowledge, ecological differences between *O. megacephalus* and *O. yunganus* have not been observed previously, but Malcolm's (1992) report of differential habitat use by *P. cuvieri* and *P. guyannensis* near Manaus agrees with our sampling results for these species. *Neacomys paracou* and *N. dubosti* occur syntopically at Paracou and are known from sympatric collections elsewhere in the Guiana subregion, but available information is too sparse to suggest how (or if) these congeners differ ecologically.

TERRESTRIAL FOLIVORE/FRUGIVORES: Three ungulate species occupy this guild at all compared inventory sites, where they account for only 4–6% of each fauna. All of the Paracou species were persecuted by local hunters and only two were actually observed by us. Our fieldnotes contain no noteworthy natural history information about either *Mazama* or *Tapirus,* but a recent analysis of tapir diets in French Guiana (Henry et al., 2000) was based in part on material collected near Paracou.

TERRESTRIAL OMNIVORES: Two members of this guild are present at Paracou, La Selva, and Manu, where they constitute an almost constant minor fraction of the known nonvolant fauna. Although both Paracou species (*Eira barbara* and *Nasua nasua*) are large, diurnal, and not locally hunted for food, neither was commonly observed in our study and no noteworthy natural history observations were recorded about them.

TERRESTRIAL ANIMALIVORES: This large and admittedly heterogeneous guild comprises a higher fraction (25%) of the fauna at Paracou than at either La Selva or Manu. Three terrestrial animalivores at Paracou are diurnal (*Monodelphis, Speothos, Galictis*), six are active both by day and at night (*Myrmecophaga, Herpailurus, Leopardus pardalis, Panthera, Puma*), and the remaining eight are nocturnal (*Marmosops parvidens, M. pinheiroi, Metachirus nudicaudatus, Dasypus kappleri, D. novemcinctus, Cabassous, Priodontes, Leopardus weidii*). All of the terrestrial-animalivorous carnivores at Paracou (felids, *Speothos,* and *Galictis*) were uncommon and most were only recorded by us through interviews. *Monodelphis, Cabassous, Dasypus kappleri, Priodontes,* and *Myrmecophaga* were likewise rarely collected, observed, or recorded from interviews. Only four local members of this guild were encountered often enough to provide noteworthy behavioral data or density estimates.

Based on their highly carnassialized dentitions, small size, and the absence of macroscopic seeds in feces, we assume that species of *Marmosops* are predominantly, if not exclusively, animalivorous. Although species of this genus have opposable halluces and prehensile tails, our nocturnal observations and trapping results suggest that *M. parvidens* and *M. pinheiroi* are predominantly terrestrial, seldom ascending slender lianas or narrow stems more than a meter or two above the forest floor; none were taken in arboreal platform traps. Malcolm (1991) likewise trapped *M. parvidens* only on the ground, despite his intensive program of arboreal platform trapping. Woodman et al. (1995) captured *M. noctivagus* equally often on the ground and above ground, but none of their above-ground traps were set higher than 2 m. Patton et al. (2000: appendix A) listed several species of *Marmosops* as having been taken in "canopy" traps at some collecting localities along the Rio Juruá in western Amazonia, but their text summaries of habitat data (op. cit.: 53–61) indicate that none were actually trapped at heights exceeding 2 m; instead, the majority (82%) of all captures of this genus on the Rio Juruá were on the ground. Because many unambiguously terrestrial mammals (including *Oryzomys, Myoprocta,* and *Proechimys* in

our study) will occasionally ascend lianas to reach baited traps, infrequent captures of *Marmosops* in low vegetation is not inconsistent with our provisional guild assignment for this genus.

Metachirus has been variously characterized in standard references as an arboreal omnivore (Walker, 1964) or a semiarboreal frugivore (Hunsaker, 1977; Streilein, 1982), but these ecobehavioral descriptors appear to be unsupported by field data. Instead, our capture results agree with observations from many other trapping programs (e.g., Miles et al., 1981; Malcolm, 1991; Patton et al., 2000) in suggesting that this is one of the most exclusively terrestrial of all New World marsupials. Similarly, our examination of stomach contents from 10 Paracou specimens is consistent with evidence from other dietary studies (Mathews, 1977; Santori et al., 1996; Freitas et al., 1997) that *Metachirus* is almost entirely insectivorous. Our nocturnal sighting rate for *Metachirus* (0.42 per 10 hours) is within the range of values reported for this taxon by Emmons (1984: table 4) at other Amazonian sites.

Semiaquatic/Riparian Folivores: This guild is not represented at Paracou, where suitable habitat for capybaras (*Hydrochoerus*) is absent. Semiaquatic-folivorous mammals never represent more than a tiny fraction of any Neotropical rainforest fauna.

Semiaquatic/Riparian Omnivores: Only a single species assignable to this guild is present at Paracou and at Manu; no ecological equivalent is known from Central American rainforests. The Paracou species (*Nectomys melanius*) is apparently very uncommon and was not trapped by us.

Semiaquatic/Riparian Animalivores: This guild comprises a smaller fraction of the fauna at Paracou than at either La Selva or Manu, where large bodies of water support resident otter populations. At Paracou, this guild is only represented by two species, both of which are nocturnal. Water opossums (*Chironectes minimus*) were sighted frequently in our study area (0.7 individuals per 10 hours of nocturnal census) and are obviously common in local streams, but we recorded no other significant natural history information about this species. Our pitfall captures of *Neusticomys oyapocki* are the first obtained by this method, which might usefully be applied to detect the presence of congeneric species at other Amazonian localities.

GENERAL DISCUSSION

Although convenient for the purposes of data analysis and publication, our separate treatments of the bats and nonvolant mammals from Paracou provide an incomplete picture of the fauna as a whole. For example, taxonomically comprehensive estimates of local species richness have yet to be discussed and compared with those from other inventory sites, nor has it been possible until now to analyze similarities and differences between bats and nonvolant mammals in terms of their biogeographic relationships and trophic structure. Such topics bridge the separate research traditions exemplified by many previous studies of rainforest mammal faunas that have treated only bats or nonvolant species in substantive detail (e.g., Eisenberg and Thorington, 1973; Glanz, 1982; Brosset and Charles-Dominique, 1990; Janson and Emmons, 1990; Ascorra et al., 1993, 1996; Medellín, 1993; Kalko et al., 1996; Peres, 1999; Patton et al., 2000). The following discussion therefore contributes to a synthesis of mammalian diversity studies in Neotropical rainforests, an objective for which future research priorities are suggested in our final chapter.

Species Richness and Inventory Completeness

We recorded a total of 142 species of mammals at Paracou, of which 128 were captured or observed as result of our own efforts in the field from 1991 to 1994. The remaining 14 species were either recorded from interviews with local residents or were identified from museum voucher material collected in our study area by previous researchers. Because our total species accumulation results (fig. 91) do not indicate a convincing asymptote, it is reasonable to assume that we could have recorded more species at Paracou with additional fieldwork, perhaps including some species not previously observed or collected by others.

To explore the range of plausible estimates

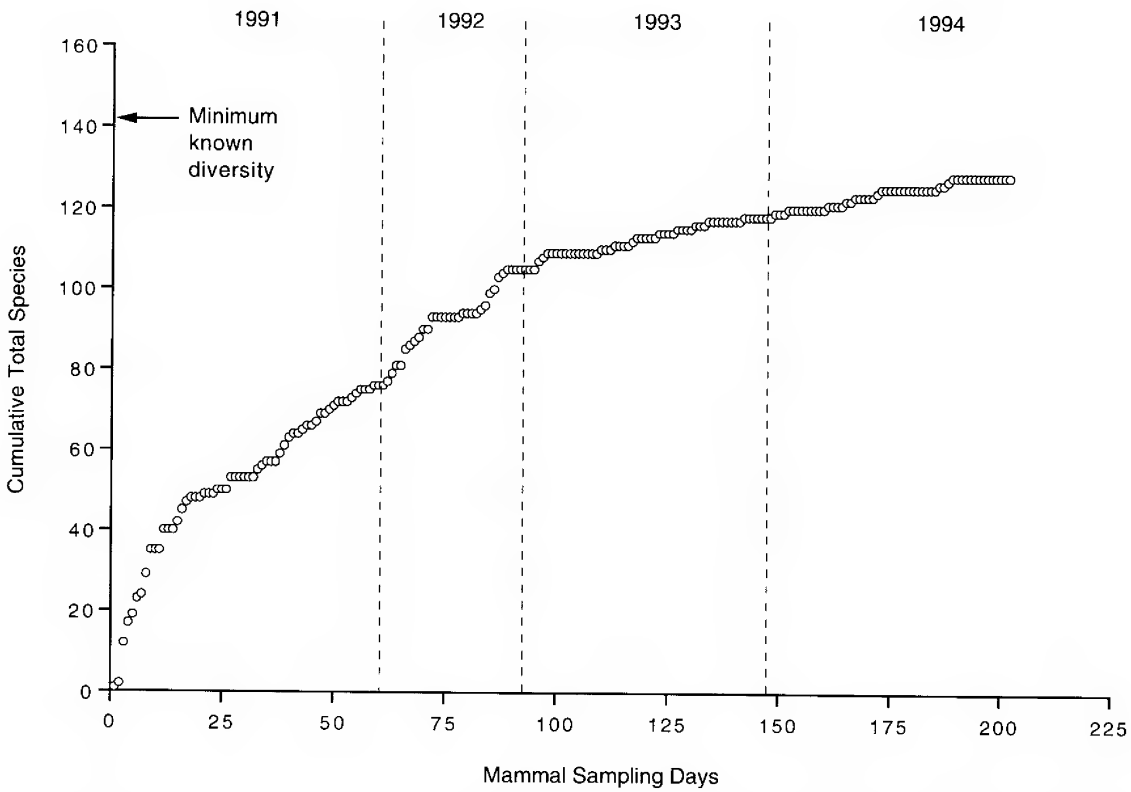

Fig. 91. Species accumulation for all mammals at Paracou, where we recorded 128 species in the course of 202 field days from 1991 to 1994. "Minimum known diversity" (142 species) includes additional records obtained from interviews, together with specimens previously collected in our study area by other investigators.

of true species richness for the entire Paracou mammal fauna, we summed the results of four nonparametric extrapolation methods applied separately[28] to our sampling data for bats and nonvolant mammals (table 60). Given the inherent uncertainty of any extrapolation procedure, it is encouraging that the range of total richness values predicted by these methods is really quite narrow (155–168 spp.). The results from Chao's methods should probably be interpreted as lower bounds for plausible inference from our data because sampling effort was sufficiently intensive that most species were each observed three or more times (i.e., information in the larger frequency classes is "nonnegligible" sensu Chao [1984, 1987]). By contrast, the jackknife methods yield statistically consistent estimators (Burnham and Overton, 1979) that should converge on true species richness as sampling effort increases. In fact, the numbers of species for bats, nonvolant mammals, and total mammals predicted by the second-order jackknife (in the fifth column of table 60) are very close to ecogeographic expectations based on the known northern French Guianan source fauna.

Estimating the overall completeness of our mammal inventory clearly depends on which of these extrapolations of true species richness is used. Whereas Chao's methods suggest completeness values (observed/extrapolated species richness × 100) in the range of 90–92%, the jackknife methods suggest low-

[28] It makes sense to perform separate extrapolations and sum the results because bats and nonvolant mammals were sampled with different methods on different schedules. In effect, however, extrapolations based on the pooled data for bats and nonbats are very close to the tabulated values using Chao's methods (157 spp. for CHAO1, 156 spp. for CHAO2) and are identical with the tabulated values using the jackknife estimators.

TABLE 60
Observed and Extrapolated Mammalian Species Richness at Paracou Compared with Expectations from Ecogeographic Range Data

		Extrapolated[a]				Expected[b]	
	Observed	CHAO1	CHAO2	JACK1	JACK2	NFG only	Surinam and FG
Bats	78	86	86	91	94	93	103
Nonvolant	64	72	69	72	74	73	75
Total	142	158	155	163	168	166	178

[a] Numbers of species predicted by the following nonparametric estimators: CHAO1, the method described by Chao (1984); CHAO2, the method described by Chao (1984) as modified for analyzing presence/absence among samples by Colwell and Coddington (1994); JACK1, the first-order jackknife (Burnham and Overton, 1979; Heltshe and Forrester, 1983); JACK2, the second-order jackknife (Burnham and Overton, 1979). Computational details for CHAO1 as applied to our bat sampling data were provided by Simmons and Voss (1998: 183), and applications of the same procedure to our nonvolant sampling data were explained earlier in this report (see Analyses of Sampling: Estimating Completeness). CHAO2, JACK1, and JACK2 were applied to our nonvolant sampling data as explained in the footnote to table 54. For applications of these methods to our bat data, we counted 13 "unicates" (species recorded on just one sampling date), 10 "duplicates" (species recorded on just two dates), and $t = 168$ total bat sampling dates.

[b] Rainforest species for which apparently suitable habitats are present at Paracou, and that occur in one or both of two potential source faunas. "NFG only" counts just those ecologically expected species actually known from northern French Guiana, whereas "Surinam and FG" counts additional species known from southern French Guiana and from Surinam. Expected species of bats are based on ecogeographic data summarized by Simmons and Voss (1998: appendix 1) excluding four French Guianan records now known to have been based on misidentified material (*Platyrrhinus lineatus, Vampyressa bidens, Vampyressa melissa, Vampyressa pusilla*; P. Charles-Dominique, personal commun.). Expected species of nonvolant mammals are based on ecogeographic data summarized in this report (appendix 1).

er values of about 85–87%. These differences are not large, however, and even the lowest estimate (based on the second-order bootstrap) suggests that the mammal fauna at Paracou is at least as well sampled as those at Central American field stations with decades-long histories of biological research. For example, faunal sampling at La Selva is perhaps only 85% complete after more than 30 years of field research at that site, whereas faunal sampling near Barro Colorado Island is perhaps only 78% complete after more than 70 years (Voss and Emmons, 1996: table 10).

Bats constitute about 55% of the known Paracou mammal fauna, and our extrapolations suggest that similar proportions (54–56%) would have been obtained with additional sampling effort. In order of decreasing richness, rodents are clearly a distant second to bats, representing only 15% of the observed total species, followed by marsupials (8%), carnivores (7%), xenarthrans (6%), primates (4%), and ungulates (4%). The small list of expected nonvolant species (appendix 1) suggests that this rank ordering by relative diversity is unlikely to change significantly with additional fieldwork in our study area.

The taxonomic dominance of bats in Neotropical rainforest mammal faunas is evidenced by all large species lists obtained with modern collecting methods (table 61), but bats may be proportionately more diverse or less diverse at some localities than they are at Paracou. Wilson (1990) suggested that bats probably represent about 60% of the fauna at La Selva, a somewhat higher figure than is supported by observed species counts from that site, but approximately what could be expected there based on ecogeographic range data (Voss and Emmons, 1996: appendix 2). Similar proportions will perhaps be found to characterize other Central American faunas, where most nonvolant clades (notably marsupials, primates, and rodents) are conspicuously less diverse than in Amazonia. By contrast, bats may constitute a smaller proportion of western Amazonian mammal faunas, where many nonvolant clades are maximally diverse. Bat communities have not been intensively sampled over multiple years at any western Amazonian site, however, with the result that existing species

TABLE 61
Bat and Nonvolant Species Richness at Ten Neotropical Rainforest Inventory Sites[a]

	Bats	Nonvolant	Total
Central America			
La Selva	65 (56%)	52 (44%)	117
Barro Colorado	66 (57%)	49 (43%)	115
Amazonia			
Imataca	62 (54%)	52 (46%)	114
Paracou	**78 (55%)**	**64 (45%)**	**142**
Arataye	61 (47%)	68 (53%)	129
Cunucunuma	50 (53%)	44 (47%)	94
Xingu	47 (49%)	48 (51%)	95
Balta	56 (43%)	74 (57%)	130
Manu	60 (43%)	79 (57%)	139
Cuzco Amazónico	44 (43%)	59 (57%)	103

[a] See figure 88 for site map and table 55 for references. Only inventories where bats and nonvolant species were sampled within the same geographic limits are tabulated. Table entries are numbers of observed species followed parenthetically by percent representation in the known fauna at each site.

counts (e.g., from Balta, Manu, and Cuzco Amazónico; table 61) probably underestimate relative bat diversity. Based on expected species lists (Voss and Emmons, 1996: appendices 9–11) it seems likely that bats will eventually be found to comprise about 50% of the total mammal fauna at most western Amazonian localities.

Although a few more mammalian species are currently known from Paracou than from any other Neotropical rainforest site for which published faunal lists are currently available (table 61, last column), this result is hard to interpret due to inventory differences in many of the confounding factors previously discussed in our comparative analyses of bat and nonvolant species richness. Among such factors, sampling methods and effort seem likely to be the most important: because we used many inventory methods over multiple field seasons at Paracou, our species list could be artifactually larger than those from more diverse sites where faunal sampling was substantially less complete.

Species accumulation graphs from our first (1991) field season at Paracou and from methodologically comparable fieldwork on the lower Rio Xingu (in southeastern Amazonia) and at Balta (in western Amazonia) tend to support this interpretation (fig. 92). For any specified level of sampling effort after the first several person-weeks at each site, the number of species recorded at Balta is consistently higher than that recorded on the Rio Xingu, which in turn is consistently higher than that recorded at Paracou. Therefore, the large species list we eventually obtained at Paracou is plausibly explained by our prolonged total sampling effort (634 person-days), and by our subsequent use (after 1991) of more methods to capture elusive species.

It is noteworthy that the rank-ordering of inventory sites by species richness implied by figure 92 is the same as that expected from geographic range data, which predict maximal mammalian diversity in the western part of Amazonia, intermediate diversity in the southeast, and minimal diversity in the Guiana subregion (Voss and Emmons, 1996). Although three data points are not sufficient to establish a significant correlation between expected and observed diversity, this result is consistent with other lines of evidence suggesting that the Paracou mammal community is a typically Guianan assemblage whose essential characteristics are largely determined by its biogeographic context. That context now requires more precise definition before its implications for community phenomena other than species richness can be assessed.

Biogeography

Our previous biogeographic analyses of Paracou bats and nonvolant mammals suggested that these groups show essentially similar spatial patterns of faunal relationships with other rainforest inventories. In both analyses, Paracou first clustered with other inventory sites from the Guiana subregion of Amazonia, next with sites from other Amazonian subregions, and lastly with Central American sites (Simmons and Voss, 1998: fig. 76; this report: fig. 89). Obviously, faunal similarity is correlated with geographic proximity in both datasets, but bats and nonvolant mammals differ in other quantitative biogeographic phenomena that merit further analysis.

To obtain strictly comparable biogeo-

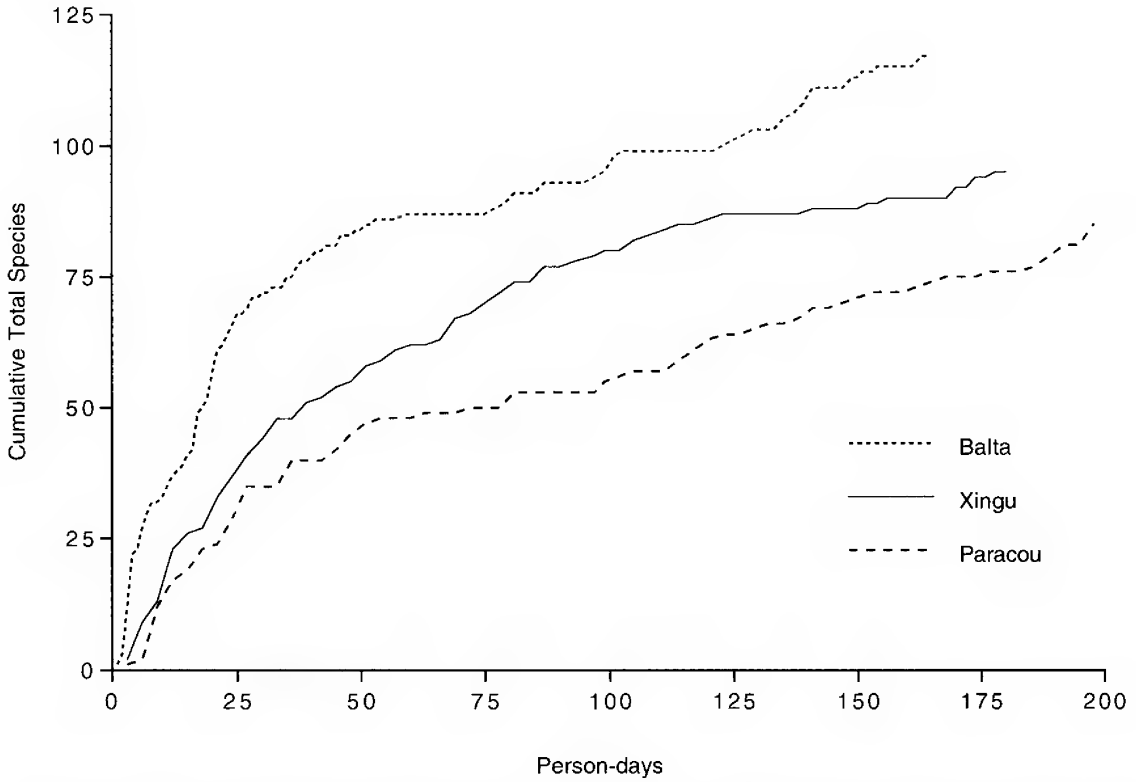

Fig. 92. Species accumulation curves for all mammals at three Neotropical rainforest inventory sites (see fig. 88). Person-days were calculated by multiplying the number of inventory workers by the number of productive field days at each site (excluding dates when no sampling occurred). The Paracou curve is from our first (1991) field season, when we used the same methods as those employed at the other localities (primarily ground-level mistnetting, searching for bat roosts, conventional trapping, and hunting/census). The Xingu curve represents collections and sight records made by USNM personnel near their base camp from 13 August to 23 October 1986 (collections at other sites up- and down-river are excluded; see Voss and Emmons, 1996: appendix 8). The Balta curve represents collections made by A. L. Gardner and J. L. Patton from 1966 to 1971, but omits miscellaneous specimens obtained at the same locality by other researchers not continuously engaged in mammal inventory work (see Voss and Emmons, 1996: appendix 9).

graphic data for bats and nonvolant mammals, we computed matrices of pairwise faunal similarity (scaled as percentages in table 62) and airline distances (table 63) among all ten inventory sites at which presence/absence data for both groups were obtained within the same study area (La Selva, Barro Colorado, Imataca, Paracou, Arataye, Cunucunuma, Xingu, Balta, Manu, Cuzco Amazónico).[29]

Among this common set of geographic samples, bat faunal similarity ranges from a minimum value of 31% (for the comparison Barro Colorado-Xingu) to a maximum of 68% (Balta-Manu), with a mean of 46% and a standard deviation of 9%. By contrast, nonvolant faunal similarity ranges from 10% (for La Selva-Xingu) to 78% (Paracou-Arataye), with a mean of 34% and a standard deviation of 16%. At this spatial scale (airline distances

[29] Manaus was omitted from these computations because the bat list was compiled from collections made at widely scattered sites around the city (Reis and Peracchi, 1987), whereas the nonvolant mammal list was based on geographically restricted sampling within the MCSE Reserves (Voss and Emmons, 1996: appendix 7). Other inventory sites omitted from these matrix calculations are those from which only bat or nonvolant mammal data are available (Jenaro Herrera, Kartabo, Piste St.-Élie).

TABLE 62

Percent Similarity among Bat and Nonvolant Mammal Faunas at Ten Neotropical Rainforest Inventory Sites[a]

(Table entries are Jaccard's coefficient × 100.)

LSe	—	64	46	42	33	32	32	33	40	33
Bco	58	—	44	38	36	36	31	37	43	35
Ima	21	25	—	56	52	49	47	49	51	45
Par	20	21	61	—	62	44	49	44	45	39
Ara	20	23	69	78	—	56	50	46	46	42
Cun	17	18	43	41	46	—	43	43	53	40
Xin	10	16	33	36	38	28	—	49	51	47
Bal	24	28	37	36	38	30	22	—	68	64
CCP	21	26	31	29	32	26	22	76	—	65
CAm	24	24	31	29	31	26	23	65	63	—
	LSe	BCo	Ima	Par	Ara	Cun	Xin	Bal	CCP	CAm

[a] Bat faunal comparisons are shown above the diagonal, nonvolant faunal comparisons below. Inventory sites are abbreviated as in table 56, and the calculation of Jaccard's coefficient is explained in the caption to figure 89. Percent similarity values for bat faunal comparisons were calculated from the presence/absence data tabulated by Simmons and Voss (1998: appendix 2) with the following corrections for Arataye (P. Charles-Dominique, personal commun.): *Rhynchonycteris naso* (0→1), *Lichonycteris obscura* (0→1), *Micronycteris microtis* (0→1), *Platyrrhinus lineatus* (1→0), *Vampyressa bidens* (1→0), *Vampyressa melissa* (1→0), *Vampyressa pusilla* (1→0), *Molossops paranus* (0→1). Percent similarity values for nonvolant faunal comparisons were calculated from the presence/absence data tabulated in appendix 2 of this report.

among these sites range from 136 to 3788 km with a mean of 2038 km and a standard deviation of 954 km), bat faunas are therefore more similar to one another (on average) and are less variable in composition than nonvolant mammal faunas.

Matrix correlations (assessed for statistical significance by random permutations; Smouse et al., 1986) indicate that the inverse relationship between faunal similarity and airline distance is equally strong for bats ($r = -0.81$, $p = 0.001$) and nonvolant mammals ($r = -0.82$, $p = 0.001$), but faunal similarity declines with distance at different average rates for the two groups (figs. 93, 94). Linear regression suggests that faunal divergence averages about 14% per 1000 km for nonvolant mammals, almost twice the estimated rate of about 8% per 1000 km for bats. In addition, the residual variance in faunal similarity values—the variation "unexplained" by airline distance—is substantially greater for nonvolant mammals than it is for bats, with an F-ratio (computed from the mean-squared-error estimates of the respective regressions) of about 2.8.

TABLE 63

Matrix of Airline Distances (km) among Ten Neotropical Rainforest Inventory Sites[a]

Bco	388								
Ima	2452	1989							
Par	3379	3004	1023						
Ara	3435	3037	1076	136					
Cun	2131	1656	649	1458	1456				
Xin	3788	3315	1613	994	859	1664			
Bal	2652	2320	2281	2714	2636	1664	2220		
CCP	2829	2508	2454	2838	2754	1847	2284	200	
CAm	2995	2655	2428	2732	2640	1849	2119	346	223
	LSe	BCo	Ima	Par	Ara	Cun	Xin	Bal	CCP

[a] Site names abbreviated as in table 56.

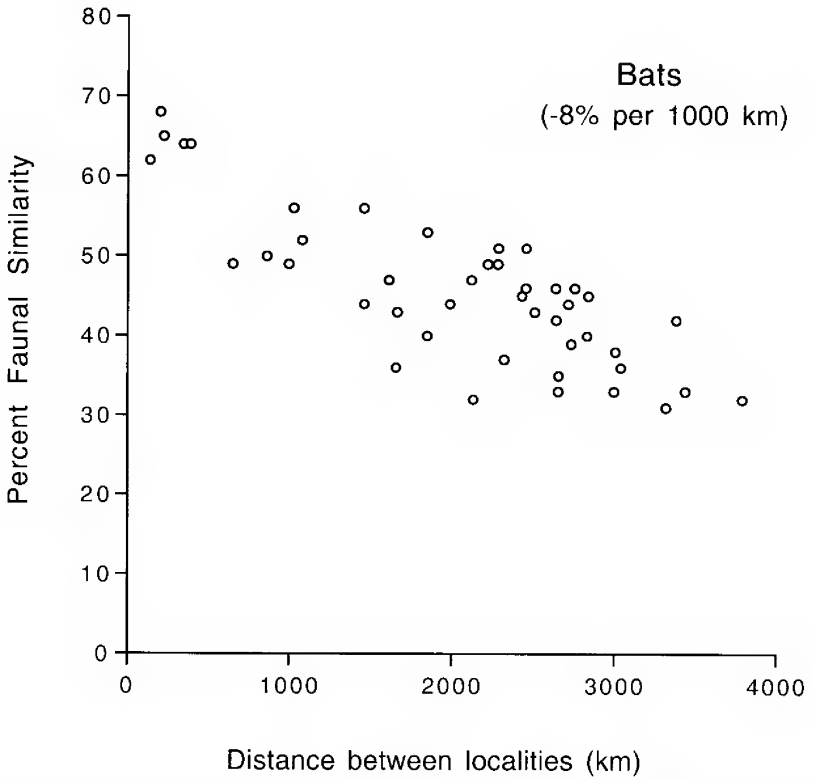

Fig. 93. Percent faunal similarity (Jaccard's coefficient of faunal similarity × 100) plotted against airline distance for all 45 pairwise comparisons among ten rainforest bat inventories (tables 62, 63).

The magnitude of the residual variation in nonvolant faunal similarity is aptly illustrated by comparisons between Paracou and two almost equidistant inventory sites. Although Imataca is slightly further from Paracou (1023 km) than is Xingu (994 km), percent nonvolant faunal similarity between Paracou and Imataca is 61%, whereas nonvolant faunal similarity between Paracou and Xingu is only 36%. Of course, faunal similarity values estimated from incomplete inventory data are subject to sampling error, which plausibly accounts for some differences between the Paracou and Xingu species lists (many ubiquitous carnivore taxa, for example, were not recorded by USNM fieldworkers during their short visit to the Xingu site; Voss and Emmons, 1996: appendix 8). An additional factor of obvious importance, however, is the role of the lower Amazon as a barrier to nonvolant faunal exchange: at least 23 of the mismatches (species present in one fauna but not the other) between the Paracou and Xingu lists are taxa with eastern Amazonian ranges that are wholly or largely restricted to either the north side of the Amazon (e.g., *Bradypus tridactylus, Saguinus midas, Alouatta seniculus, Ateles paniscus, Pithecia pithecia, Oecomys auyantepui, Oecomys rutilus, Coendou melanurus, Proechimys guyannensis*) or to the south side (e.g., *Bradypus variegatus, Saguinus niger, Alouatta belzebul, Aotus infulatus, Callicebus moloch, Oecomys paricola, Oryzomys emmonsae, Oxymycterus amazonicus, Proechimys goeldii, Proechimys oris*). By contrast, bat faunal similarity does not differ dramatically between Paracou-Imataca (56%) on the one hand and Paracou-Xingu (49%) on the other, and only two bat species appear to have range limits defined by the lower Amazon (*Tonatia schulzi* and *Lasiurus atratus,* both known only from the north side). The same set of inventory comparisons therefore suggests that major rivers and other large-scale habitat discontinuities are less effective as

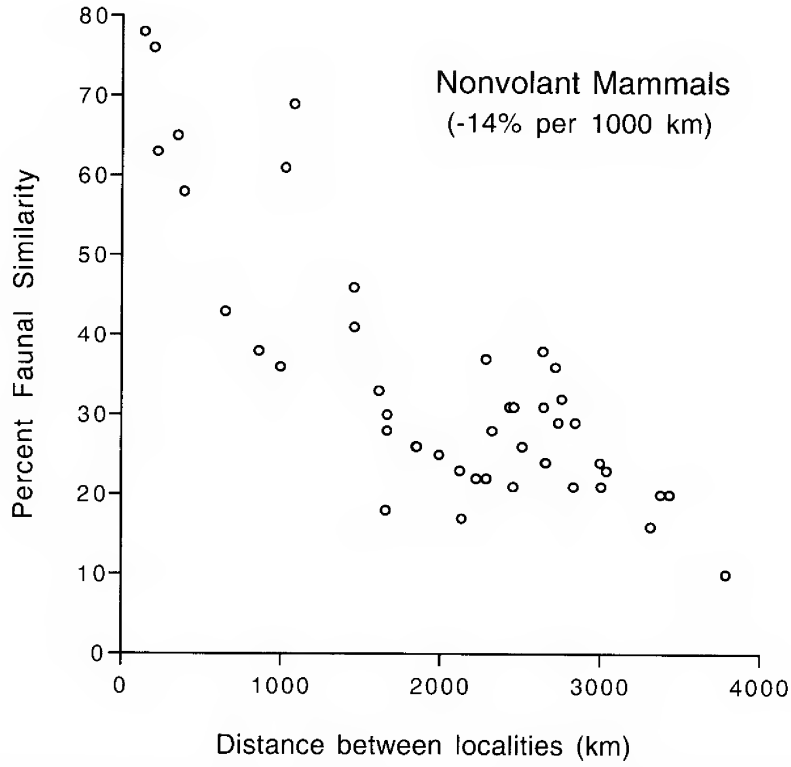

Fig. 94. Percent faunal similarity (Jaccard's coefficient of faunal similarity × 100) plotted against airline distance for all 45 pairwise comparisons among ten nonvolant rainforest mammal inventories (tables 62, 63).

dispersal barriers for bats than for nonvolant mammals.

Different average dispersal abilities of bats on the one hand and nonvolant mammals on the other could explain the disparate results of regressing faunal similarity on airline distance for these groups. Because widely separated localities will usually have more intervening barriers between them than adjacent localities, faunas composed of taxa with lower average dispersal abilities should diverge more rapidly with distance (on average) than faunas composed of more vagile taxa. However, because barriers sometimes do occur between nearby sites (as those on opposite river banks), the residual variance should also be larger for faunas composed of taxa with lower average dispersal abilities.

Patterns of species distribution among Neotropical rainforest regions separated by high mountains, major rivers, and xeromorphic vegetation (fig. 95) are consistent with the hypothesis that large-scale habitat discontinuities are less effective as faunal barriers for bats than they are for nonvolant mammals. Thus, most Paracou bats (42 species, representing 54% of the local chiropteran fauna; table 64) occur in all four Neotropical rainforest regions, another 19 bat species (24%) occur in three out of four rainforest regions, and an additional 11 species (14%) occur in two regions. Altogether, 92% of Paracou bats are apparently undifferentiated across one or more major landscape features delimiting the Neotropical rainforest biota. Only six species (about 8% of the local chiropteran fauna) are Amazonian endemics.

Nonvolant Paracou mammals show contrasting patterns of species membership in these distributional categories, especially the first and last. Only 18 species (comprising just 28% of the nonvolant fauna) occur in all four Neotropical rainforest regions, whereas 24 species (fully 38% of the nonvolant fauna) are Amazonian endemics. To facilitate statistical testing of these frequency differ-

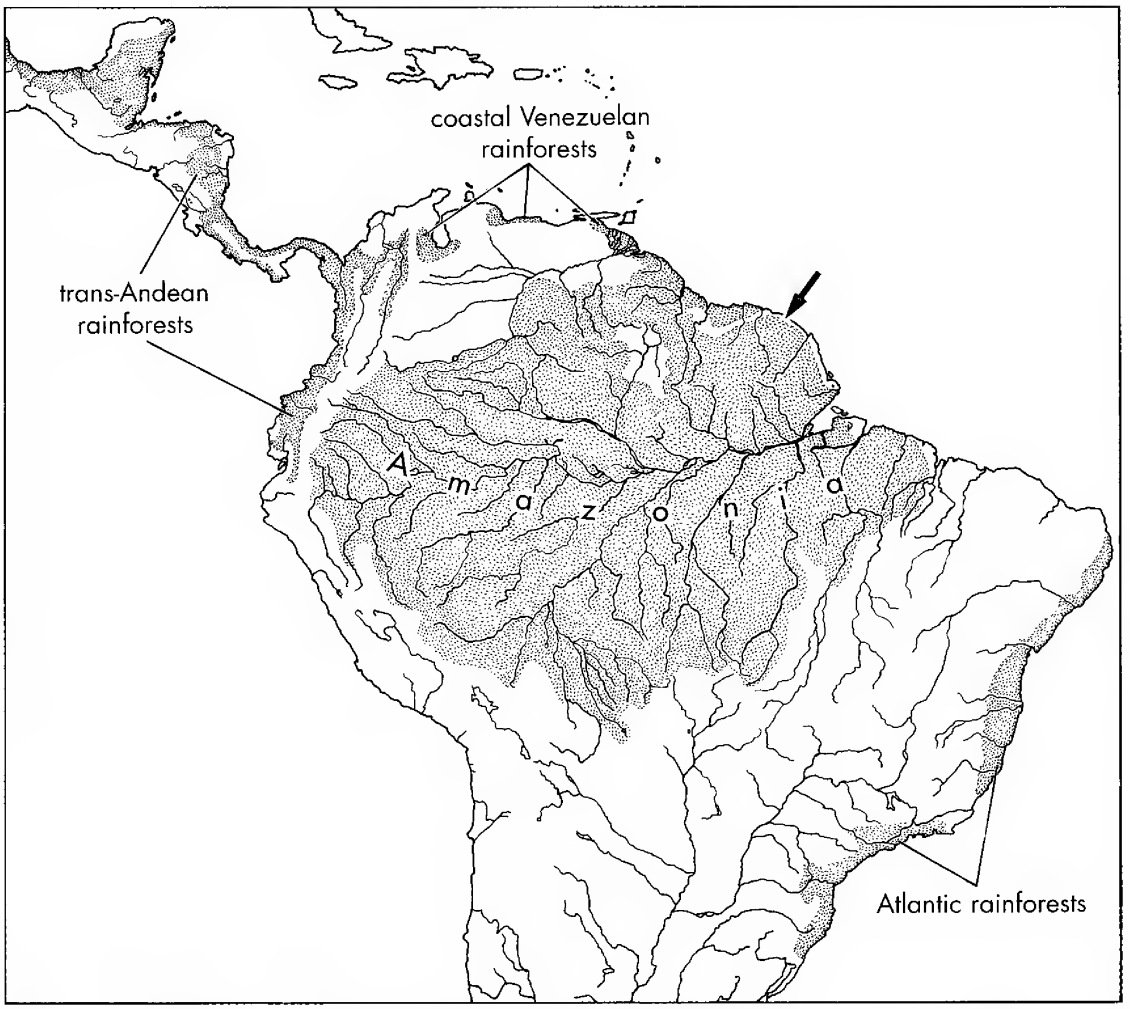

Fig. 95. Distribution of lowland rainforest on the Central and South American mainland (see Voss and Emmons, 1996, for references). Major habitat discontinuities delimit four distinct regions: (1) the Andes and the Serranía de Perijá separate trans-Andean rainforests to the west from Venezuelan coastal rainforests and Amazonian rainforests to the east; (2) the Llanos and the lower Orinoco separate Venezuelan coastal rainforests to the north and west from Amazonia to the south and east; (3) an arid diagonal of xeromorphic biomes (Caatinga, Cerrado, Chaco) separates Amazonia to the northwest from the Atlantic rainforests (Mata Atlantica) to the southeast. The location of our inventory site at Paracou is indicated by the arrow.

ences, we dichotomously classified all Paracou mammals as either "widespread" (present in two or more rainforest regions) or "endemic" (restricted to Amazonia). The hypothesis that Paracou bats and nonvolant mammals do not differ in relative endemism (and implied dispersal ability) can be confidently rejected based on the resulting 2×2 contingency analysis (table 65).

To explore the geographic structure of endemism in rainforest bats and nonvolant mammals, we applied biogeographic parsimony methods (as originally described by Rosen, 1988, 1992) to identify repeated patterns of species-sharing among inventory sites. Parsimony analyses of endemism (PAE) were implemented with heuristic search algorithms in PAUP* (version 4.0b3a; Swofford, 2000), which were applied separately to the presence/absence data for bats

TABLE 64
Comparative Rainforest Distribution Patterns of Paracou Bats and Nonvolant Mammals

Distribution pattern[a]	No. of species	
	Bats[b]	Nonvolant[c]
All four regions	42	18
All but trans-Andean	5	7
All but coastal Venezuelan	3	1
All but Atlantic	11	4
Trans-Andean and Amazonian	2	0
Coastal Venezuelan and Amazonian	1	9
Amazonian and Atlantic	8	1
Amazonian only	6	24
Totals	78	64

[a] Recorded occurrence in the four Neotropical rainforest regions defined by Voss and Emmons (1996).

[b] Counts from Simmons and Voss (1998: table 77) but corrected to take into account coastal Venezuelan rainforest records reported by Linares (1998) for seven species previously unknown from that region (*Choeroniscus minor, Phyllostomus elongatus, Rhinophylla pumilio, Artibeus obscurus, Mesophylla macconnelli, Sturnira tildae, Thyroptera tricolor*), and new Atlantic rainforest records (Ditchfield, 1996; Silva et al., 1996; D. Faria, personal commun.) for another six species (*Micronycteris hirsuta, M. microtis, Tonatia saurophila, Artibeus gnomus,* and *Molossops abrasus*).

[c] Counts from table 57.

TABLE 65
Comparison of Endemicity in Paracou Bats and Nonvolant Mammals[a]

	Bats	Nonvolant mammals	Totals
Widespread species	72	40	112
Amazonian endemics	6	24	30
Totals	78	64	142

$\chi^2 = 18.7$, df = 1, $p \ll 0.01$

[a] Table entries are numbers of species. Widespread species (those that occur in two or more rainforest regions) and Amazonian endemics are based on distributional frequencies from table 64.

and nonvolant mammals; an all-zero operational geographic unit was added to both datasets to root the resulting networks. Relative support for different locality groupings was estimated by bootstrap resampling with 1000 replicates using 100 random-addition sequences per replicate.

The geographic patterns recovered with ≥50% bootstrap support by PAE are a subset of those previously obtained from UPGMA clustering by Jaccard's coefficient for both datasets (figs. 96, 97). It is also noteworthy that no PAE grouping that received more than 50% bootstrap support in one dataset conflicts with any PAE grouping with equivalent support in the other. Instead, a Central American/Amazonian faunal dichotomy is indicated for both bats and nonvolant mammals, as is a well-supported grouping of three adjacent inventory sites in southwestern Amazonia. However, PAE based on the nonvolant data supports additional intra-Amazonian faunal relationships that are not consistently recovered by PAE from the bat data.

A spatially compact grouping of four nonvolant inventories from the coastal watershed of the Guianan subregion of Amazonia (Imataca, Kartabo, Arataye, Paracou) is recovered by PAE with moderately strong (71%) bootstrap support, but this endemicity set is immediately joined with similar (74%) support by the nonvolant inventory from Manaus, a site deep in the continental interior near the confluence of the Rio Negro and the Amazon. Although the next nonvolant inventory site to join is Cunucunuma (another deep-continental site), this grouping has only marginal (57%) bootstrap support. Finally, PAE recovers an even more inclusive grouping composed of these six sites plus the nonvolant inventory from the Rio Xingu, which joins the others with moderate (68%) bootstrap support despite its isolated position south of the Amazon.

Of course, some of this recovered structure is due to the absence of inventory data from many geographically intermediate localities. Inevitably, the addition of new faunal lists with novel combinations of species will reduce the distinctiveness of some currently well-supported groupings in future analyses. A more general criticism of these results could justifiably invoke the inappropriateness of hierarchical models for analyzing data that perhaps lack a natural hierarchical structure.[30] Certain spatial patterns recovered in

[30] This criticism, which de Queiroz and Good (1997) and others have levelled at phenetic clustering methods as conventionally used to explore the structure of similarity data, applies equally to parsimony algorithms as

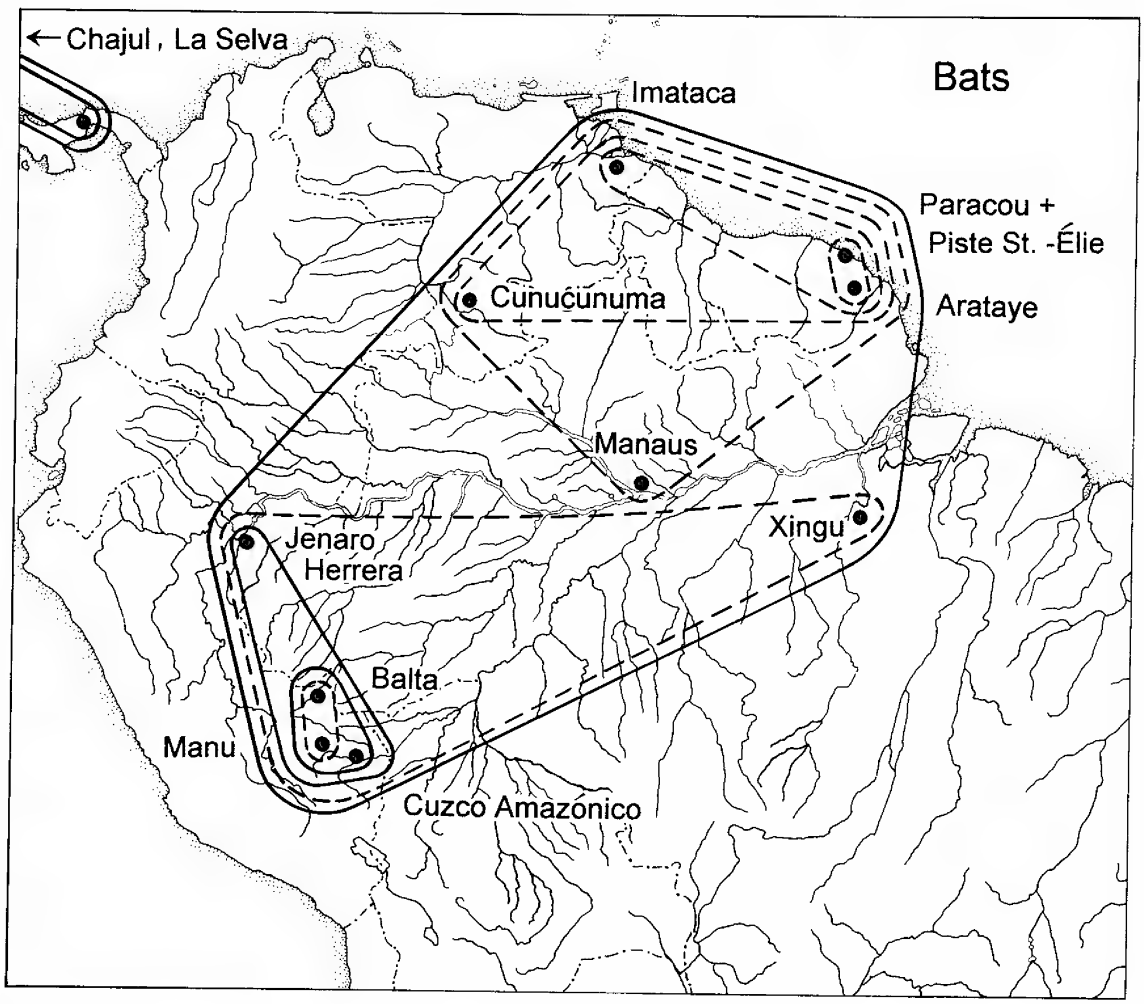

Fig. 96. Results of biogeographic analyses of 14 rainforest bat faunas (see Simmons and Voss [1998: table 75] for geographic coordinates and other locality information). Solid contours enclose groups obtained from UPGMA clustering by Jaccard's coefficient of faunal similarity that were also recovered with ≥50% bootstrap support from a parsimony analysis of endemicity (PAE; see text for explanation). Broken contours show UPGMA similarity clusters that receive <50% bootstrap support from PAE. Paracou and Piste St.-Élie (an adjacent inventory site in northern French Guiana) were treated as separate terminals (OTUs) in both analyses, but are here combined for visual clarity. The raw (presence/absence) data on which both clustering and PAE were based are those tabulated by Simmons and Voss (1998: appendix 2) with the corrections noted in table 62 of this report.

our analyses, however, are strongly supported by external evidence and seem likely to sustain meaningful biogeographic interpretation. One such pattern is the cluster of inventories that includes Paracou and most, but not all, of the other analyzed sites from the Guiana subregion of Amazonia.

Although the area enclosed by the interconnected waters of the Orinoco, the Rio Negro, and the lower Amazon has traditionally been recognized as a convenient unit for biogeographic analysis (e.g., by Tate, 1939;

←
used to reconstruct the relationships of continental faunas that may have routinely exchanged taxa by dispersal (or "dispersion" sensu Cracraft, 1994) over evolutionary time. The most that can be said for either analytic method in our applications is that the results can be mapped on geography in such a way that spatial patterns (or the absence of such patterns) in the data are readily apparent.

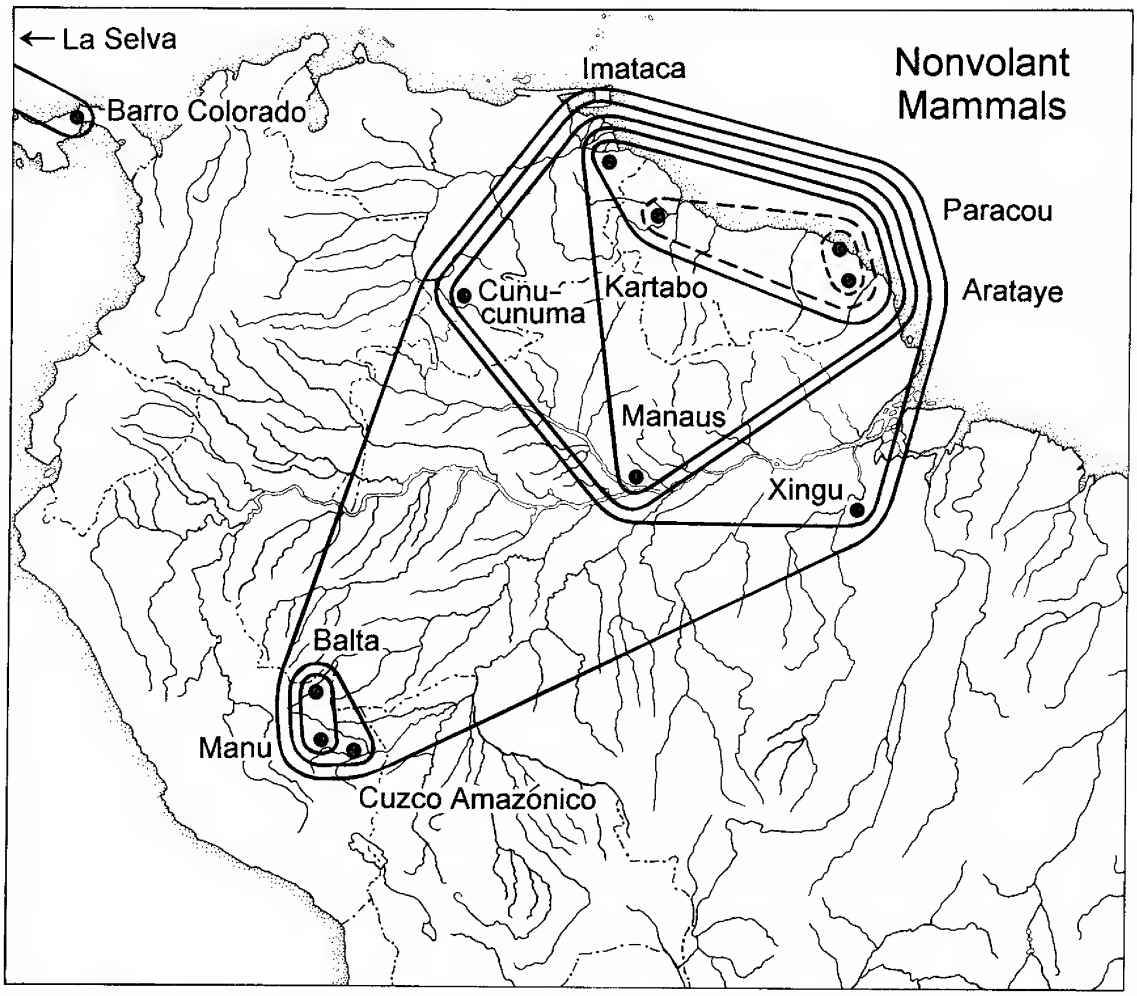

Fig. 97. Results of biogeographic analyses of 12 nonvolant rainforest mammal faunas (see table 55 for geographic coordinates and other locality information). Solid and broken contours enclosing various groups were drawn following the same conventions explained in the caption to figure 96. The raw (presence/absence) data on which both clustering and PAE were based are tabulated in appendix 2.

Hoogmoed, 1979; Mori, 1991; Voss and Emmons, 1996), the Guiana subregion of Amazonia is actually inhabited by two distinctly different rainforest mammal faunas (fig. 98). One of these consists of an apparently allochthonous (non-Guianan) assemblage that is represented by collections from Cunucunuma, Esmeralda, Boca Mavaca, Neblina Base Camp, and several other localities east of the Casiquiare in southern Venezuela. The other fauna, distinctively Guianan in taxonomic composition, is represented by collections from Imataca, Kartabo, Paracou, Arataye, Manaus, and numerous other sites in the Guianas (e.g., Dadanawa) and Guianan Brazil (e.g., Faro, Serra do Navio).

The fauna that occurs east of the Casiquiare in southern Venezuela includes at least 19 species, all of which have more-or-less extensive western Amazonian distributions (table 66). Most of these do not range much farther into the Guiana subregion, but a few have been collected or observed as far eastward as the right (west) bank of the Rio Branco, which apparently constitutes a significant geographic limit to this fauna in Brazil: *Ateles belzebuth* (see Nunes et al., 1988), *Callicebus torquatus* (Hershkovitz, 1990),

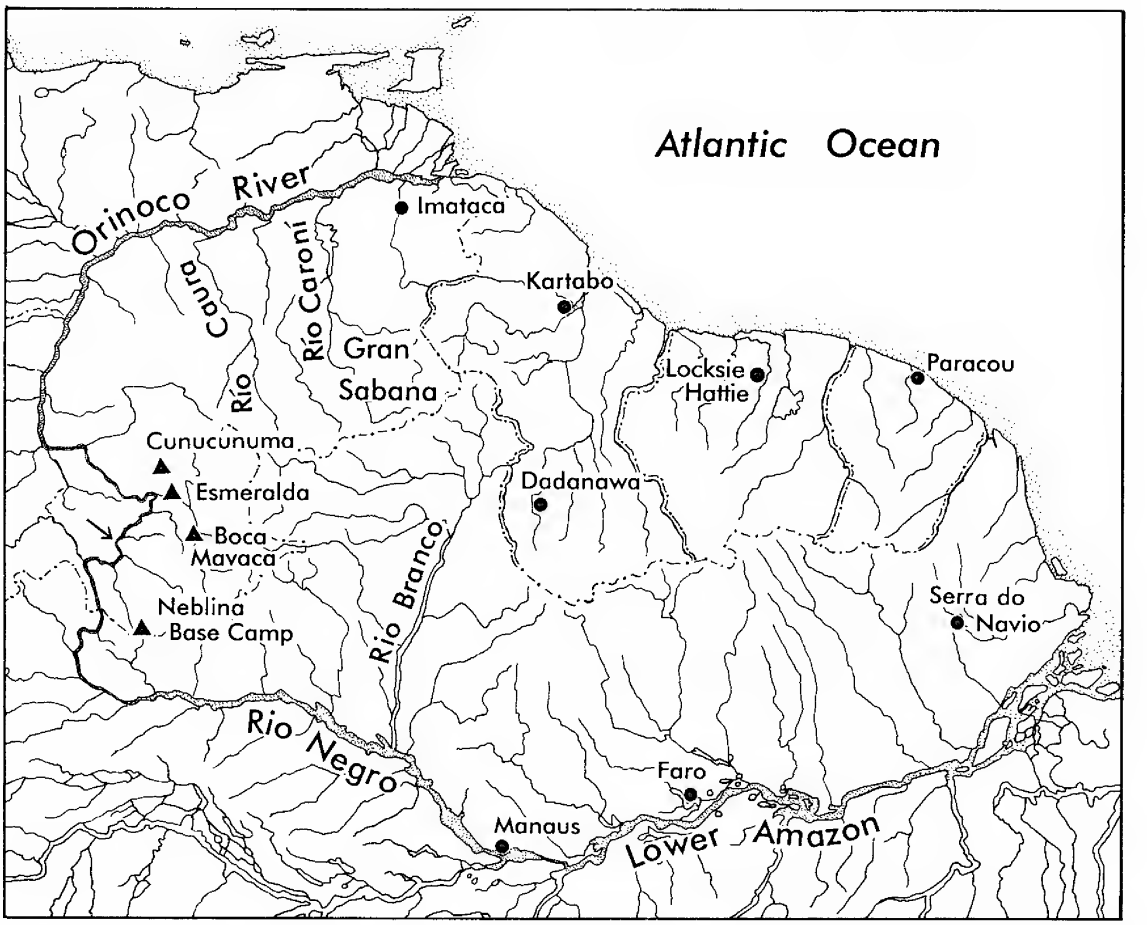

Fig. 98. The Guiana subregion of Amazonia as traditionally delimited by the Orinoco, the Rio Negro, and the lower Amazon; an arrow indicates the Casiquiare Canal, which connects the headwaters of the Orinoco and the Rio Negro in southern Venezuela. Closed circles (●) show inventory sites and other collecting localities with typically Guianan rainforest mammal faunas; triangles (▲) show localities with faunas that include many allochthonous (non-Guianan) species of rainforest mammals. Geographic coordinates and references (which list museum collections where voucher specimens are preserved) for Cunucunuma, Imataca, Kartabo, and Manaus (= MCSE Reserves) are provided in table 55. Equivalent information about three other localities is available in the literature: Esmeralda (Tate, 1939; Handley, 1976), Boca Mavaca (Handley, 1976), and Neblina Base Camp (Gardner, 1988). Collections from Dadanawa (2°50′N, 59°30′W) are in the ROM and USNM. Collections from Locksie Hattie (5°10′N, 55°28′W) are in the FMNH. Collections from the vicinity of Faro (2°11′S, 56°44′W) are in the AMNH. Collections that we examined from the Serra do Navio (0°59′N, 52°03′W) are in the USNM.

Sciurus igniventris (Emmons, 1997: map 147), and *Oecomys concolor* (G. G. Musser, personal commun.). In Venezuela, some allochthonous taxa appear to reach their eastern range limits at or near the Río Caura (e.g., *Philander andersoni, Ateles belzebuth*) or the Río Caroní (e.g., *Aotus trivirgatus, Callicebus torquatus*; Linares, 1998). Apparently, only two members of this fauna reach the left bank of the Essequibo or its upper tributaries in Guyana: *Bassaricyon gabbii* (based on the single historical record discussed by Tate, 1939) and *Caluromys lanatus* (see Emmons, 1993a).

A few other non-Guianan mammals are known from scattered localities on the north bank of the lower Amazon. These could be members of a distinctive whitewater-flood-

TABLE 66
Allochthonous (non-Guianan) Mammals that Occur East of the Casiquiare Canal in Southern Venezuela[a]

	Sources
Caluromys lanatus	Handley (1976), Gardner (1988)
Philander andersoni	Patton and da Silva (1997), Hershkovitz (1997)
Bradypus variegatus	Handley (1976)
Scleronycteris ega	Handley (1976), Ochoa et al. (1993)
Rhinophylla fischerae	Gardner (1988)
Sphaeronycteris toxophyllum	Handley (1976), Gardner (1988)
Ateles belzebuth	Handley (1976), Bodini and Pérez-Hernández (1987)
Aotus trivirgatus	Handley (1976), Gardner (1988), Bodini and Pérez-Hernández (1987)
Cacajao melanocephalus	Handley (1976), Bodini and Pérez Hernández (1987), Hershkovitz (1987b), Gardner (1988)
Callicebus torquatus	Handley (1976), Bodini and Pérez-Hernández (1987), Gardner (1988), Hershkovitz (1990)
Cebus albifrons	Handley (1976), Bodini and Pérez-Hernández (1987), Gardner (1988)
Bassaricyon gabbii	Handley (1976)
Sciurus igniventris	Tate (1939), Handley (1976), Gardner (1988)
Oecomys concolor	G. G. Musser (personal commun.)
Dasyprocta fuliginosa	Ojasti (1972), Handley (1976), Gardner (1988)
Myoprocta pratti	Tate (1939),[b] Handley (1976), Gardner (1988)[b]
Dactylomys dactylinus	Ojasti et al. (1992), Molina et al. (1995)
Isothrix bistriata	Tate (1939), Handley (1976), Patton and Emmons (1985)
Mesomys cf. *ferrugineus*	This report

[a] For the purpose of this analysis, allochthonous taxa are species with extensive distributions in other Amazonian subregions (or species belonging to genera with such distributions) that are not widely distributed in the Guiana subregion. Cited sources are those that provide the most detailed specimen or locality documentation associated with correct taxonomic identifications of Venezuelan material, except as noted.

[b] Tate and Gardner used the incorrect name *M. acouchy* for specimens of the green species that they collected in Amazonas, Venezuela.

plain biota (e.g., as mapped by Salo and Räsänen, 1989: fig. 1), the taxonomic composition of which might include both western Amazonian elements (e.g., *Gloronia venusta*; da Silva and Langguth, 1989) and central Amazonian endemics that occur on both sides of the river (e.g., *Makalata grandis*; Emmons, 1997, personal commun.). The apparently narrow distributions of *Dactylomys dactylinus* and *Bradypus variegatus* along the north bank of the lower Amazon may also be restricted to floodplain habitats.

By contrast, the remainder of the Guiana subregion (east of the Río Caroní-Rio Branco and north of the Amazonian floodplain) is inhabited by a strikingly homogeneous and unmistakably autochthonous fauna, at least 17 members of which have sufficiently congruent range limits to usefully define a Guianan center of mammalian endemism (table 67). Although a few taxa that we consider Guianan endemics are known to occur west of the Río Caroní (e.g., *Monodelphis brevicaudata, Chiropotes satanas chiropotes, Proechimys guyannensis*) or along the south bank of the lower Amazon (*Marmosops parvidens, Marmosops pinheiroi, Bradypus tridactylus, Myoprocta acouchy*), range overlap is most extensive in the core area whose periphery is suggested by the closed circles in figure 98. Other typically Guianan but nonendemic species that have similar distributional limits within the subregion include *Philander opossum* (replaced by *P. andersoni* in southern Venezuela), *Cebus olivaceus* (replaced by *C. albifrons* in southern Venezuela), *Sciurus aestuans* (replaced by *S. gilvigularis* in southern Venezuela), *Dasyprocta leporina* (replaced by *D. fuliginosa* in southern Venezuela), *Myoprocta acouchy* (replaced by *M. pratti* in southern Venezuela), and a small-toothed form of *Mesomys* with distinctive mtDNA sequences (replaced by a large-toothed congener with divergent mitochondrial genes in southern Venezuela).

This geographic segregation of distinct rainforest mammal faunas in the Guiana subregion strikingly resembles the avifaunal patterns previously mapped by Cracraft (1985: fig. 3). In particular, his concept of an "Imeri" avifauna that extends from northwestern Amazonia into southern Venezuela is consistent with our interpretation of the southern

TABLE 67
Taxa with Overlapping Geographic Distributions that Define a Guianan Center of Mammalian Endemism

	Range maps
Marmosops parvidens	This report (fig. 27)
Marmosops pinheiroi	This report (fig. 27)
Monodelphis brevicaudata	This report (fig. 28)
Bradypus tridactylus	Wetzel (1982: fig. 4), Wetzel (1985: fig. 4)
Tonatia schulzi	Unpublished[a]
Lasiurus atratus	Unpublished[b]
Saguinus midas (s.s.)	Hershkovitz (1977: fig. X.46)[c]
Ateles paniscus (s.s.)	Kellogg and Goldman (1944: fig. 1), Norconk et al. (1996: fig. 4)
Chiropotes satanas chiropotes	Hershkovitz (1985: fig. 1), Norconk et al. (1996: fig. 5)
Pithecia pithecia	Hershkovitz (1987c: fig. 1), Norconk et al. (1996: fig. 5)
Neacomys paracou	This report (fig. 41)
Oecomys auyantepui	This report (fig. 54)
Oecomys rex	Unpublished[e]
Oecomys rutilus	This report (fig. 60)
Coendou melanurus	This report (fig. 66)
Proechimys guyannensis	Unpublished[f]
Myoprocta acouchy	This report (fig. 73)

[a] Published locality records for *Tonatia schulzi* are from Guyana (McCarthy and Handley, 1987; Lim and Engstrom, in press), Surinam (Genoways and Williams, 1980), French Guiana (McCarthy et al., 1988; Brosset and Charles-Dominique, 1990; Voss and Emmons, 1996: appendix 5; Simmons and Voss, 1998), and Brazil (north of the lower Amazon and east of the Rio Branco; Marques and Oren, 1987; Gribel and Taddei, 1989).

[b] Handley's (1996) original description of *Lasiurus atratus* cited locality records from northeastern Venezuela, Surinam, and French Guiana. The species has subsequently been collected near Manaus (C. O. Handley, Jr. and E. Kalko, personal commun.) and in Guyana (Lim et al., 1999).

[c] Recent primatological survey work in Brazil suggests that *Saguinus midas* does not occur west of the Rio Branco (contra Hershkovitz, 1977; see Nunes et al., 1988).

[d] Recent primatological survey work in Brazil suggests that *Pithecia pithecia* does not occur west of the Rio Branco (contra Hershkovitz, 1987c; see Nunes et al., 1988). The single record of *P. pithecia* from southern Venezuela (Cunucunuma) reported by Handley (1976) and subsequently remarked as an anomalous outlier by various authors (Bodini and Perez-Hernández, 1987; Norconk et al., 1995; Linares, 1998) is based on two specimens, identified in the field, that were lost during transshipment in Caracas (C. O. Handley, Jr., personal commun.). Given the allochthonous affinities of many southern Venezuelan primates, the possibility that those specimens were examples of the western Amazonian species *P. monachus* cannot be discounted.

[e] We have examined specimens of *Oecomys rex* (cited by museum catalog number in table 27) from eight localities in Guyana, French Guiana, and Brazil (north of the Amazon and east of the Rio Branco; additional material is known from northeastern Venezuela (Ochoa et al., 1993) and Surinam (G. G. Musser, personal commun.).

[f] See the systematic account for *Proechimys guyannensis* in this report for a discussion of probable range limits.

Venezuelan mammal fauna as essentially non-Guianan.[31] Likewise, his "Guyanan" center of avian endemism appears to be geographically identical with our similarly named mammalian center. Such congruence invites yet wider organismal comparisons to test the generality of these results.

Only a few relevant compilations of distributional data are available for other higher taxa, but several show similar geographic patterns. In particular, mapped range limits for rainforest lizards (Dixon, 1979: fig. 9:8), snakes (Dixon, 1979: fig. 9:9), and Lecythidaceae (Mori, 1991: fig. 1) suggest that most Guianan endemics in these groups likewise do not occur west of the Río Caroní and the Rio Branco. Possibly, the broad lower reach-

[31] Few mammals can be confidently identified as Imeri endemics (sensu Cracraft, 1985) based on current taxonomic revisions. Although possible examples include *Saguinus inustus* (mapped by Hershkovitz, 1977: fig. X.15), *Aotus trivirgatus* (see Hershkovitz, 1983: fig. 2), and *Cacajao melanocephalus* (see Hershkovitz, 1987b), most mammals that occur in the Imeri region seem to be widespread in other parts of western Amazonia.

es of both rivers—together with the mostly savanna-covered highlands from which they arise—have been historically effective barriers to faunal and floral exchange between the rainforested Imeri and Guyana lowlands. Alternatively (or additionally), these rivers might approximate the geographic limits of some distinctive combination of soils and climate to which the endemic Guianan rainforest biota is uniquely adapted. Whatever historical and/or contemporary-ecological factors might explain this phenomenon, however, it seems clear that the Guianan center of mammalian endemism is part of a general pattern of biotic differentiation shared with other sympatric groups of rainforest organisms.

The Paracou mammal fauna is a typically Guianan assemblage that includes at least 14 of the 17 endemics listed in table 67 together with many nonendemic but typically Guianan species (e.g., *Philander opossum, Ametrida centurio, Sciurillus pusillus, Dasyprocta leporina*). Although we recorded a few taxa at Paracou that were previously unknown as elements of the Guianan fauna (*Hyladelphys kalinowskii, Saccopteryx gymnura, Micronycteris homezi, M. schmidtorum*), these are more plausibly interpreted as widespread but elusive species than as biogeographic anomalies. By contrast, most of the other mammals we recorded at Paracou are known from numerous additional Guianan localities from Imataca or Kartabo to Manaus and the Serra do Navio.

The biogeographic character of the Paracou fauna is equally apparent, however, in our failure to record many taxa that are widespread in western and/or southeastern Amazonia. In fact, the shared absence of such species as *Glossophaga comissarisi, Carollia castanea, Rhinophylla fisherae, Enchisthenes hartii, Platyrrhinus infuscus, Sphaeronycteris toxophyllum, Sturnira magna,* and *Uroderma magnirostrum* more readily characterizes Guianan bat inventories (and accounts for their cohesion in faunal cluster analyses) than does the shared presence of such rare endemics as *Tonatia schulzi* and *Lasiurus atratus.* Among nonvolant Amazonian inventories, the shared absence of *Callithrix, Cebuella, Cacajao, Callicebus, Lagothrix, Bassaricyon, Microsciurus,* giant squirrels (*Urosciurus*), *Scolomys,* and *Dactylomys* is likewise uniquely Guianan.

Of course, mammalian faunal composition is not constant within the Guianan center. For example, some species that have been recorded near Kartabo (e.g., *Neacomys guianae*; table 19, footnote *b*) or Manaus (*Saguinus bicolor*; Hershkovitz, 1977: fig. X15) are not known to occur in French Guiana. Similarly, a few species that we collected at Paracou are currently known only from additional sites in French Guiana, Amapá, or eastern Surinam (*Molossus barnesi, Neacomys dubosti, Neusticomys oyapocki*). Such narrowly distributed taxa suggest the existence of subcenters of mammalian endemism, perhaps corresponding in location to several of the "refugia" that Prance (1982: fig. 11.9) postulated to explain distributional phenomena in the Guianan rainforest flora. In particular, Prance's "East Guianan" endemics—rainforest plants with small ranges centered on French Guiana and Amapá (e.g., *Corythophora amapaensis*; see Mori and Prance, 1987: fig. VI-1)—may represent elements of the same narrowly endemic biota that we sampled at Paracou and share the same history of geographic isolation and/or local adaptation. Much future collecting, however, will be required to convincingly document geographic range limits for East Guianan endemic mammals, which do not appear to account for more than a small fraction (about 2%) of the Paracou fauna.

Community Structure

Using the information previously summarized in our separate guild analyses of bats and nonvolant species, we classified all Paracou mammals by diel activity (nocturnal, diurnal, both), substrate use (aerial, arboreal, terrestrial, semiaquatic), and trophic role (primary consumers, secondary consumers, omnivores) to examine basic aspects of community-wide patterns of resource use (table 68). Obviously, a more complete ecological representation of the entire fauna could be obtained by cross-classifying species using the same criteria (e.g., to count diurnal-arboreal primary consumers, nocturnal-terrestrial secondary consumers, etc.) and by taking other physiologically significant traits

TABLE 68
Summary Ecobehavioral Traits of Paracou Mammals

	No. of species
Diel activity[a]	
Nocturnal	115 (81%)
Diurnal	18 (13%)
Both	9 (6%)
Substrate use[b]	
Aerial	78 (55%)
Arboreal	27 (19%)
Terrestrial	34 (24%)
Semiaquatic	3 (2%)
Trophic level[b]	
Primary consumers	55 (39%)
Secondary consumers	73 (51%)
Omnivores	11 (8%)
Unknowns	3 (2%)

[a] Diurnal taxa include *Monodelphis*, primates, *Bradypus*, *Speothos*, *Eira*, *Galictis*, *Nasua*, tayassuids, sciurids, and dasyproctids. Taxa that are active both by day and at night include *Myrmecophaga*, *Tamandua*, *Herpailurus*, *Leopardus pardalis*, *Panthera*, *Puma*, *Tapirus*, and *Mazama*. All other taxa are nocturnal.

[b] Table entries are based on guild assignments summarized by Simmons and Voss (1998: table 79) and this report (table 59). Note that arboreal species in our tabulations include species described as "scansorial" by others (e.g., Fleming, 1973; Bourlière, 1989; Kay and Madden, 1997). Primary consumers include frugivores, nectarivores, granivores, folivores, and herbivores; secondary consumers include insectivores, "animalivores," piscivores, and sanguivores.

TABLE 69
Comparison of Trophic Structure between Rainforest Mammal Communities at Two Amazonian Localities[a]

	Localities		
	Paracou	Manu	Totals
Primary consumers	55	78	133
Secondary consumers	73	49	122
Totals	128	127	255

$\chi^2 = 8.7$, df = 1, $p < 0.01$

[a] Table entries are numbers of species based on guild assignments tabulated by Simmons and Voss (1998: table 79) and in this report (table 59) following the conventions explained in the footnotes to table 68.

(such as body weight) into account. However, faunal analyses based on such comprehensive treatments are dauntingly complex (Skalli and Dubost, 1986; Dubost, 1987) and beyond the scope of this report. For many ecological researchers, the appropriate units of community analysis represent biomass (e.g., kg/km^2; Eisenberg and Thorington, 1973; Janson and Emmons, 1990; Peres, 1999) rather than species, but taxonomic diversity (not energy flow) is the subject of interest in the following discussion.

The Paracou fauna does not appear to be unusual with respect to patterns of either diel activity or substrate use if allowance is made for the undersampling of bats in most Neotropical rainforest inventories on which previous conjectures about whole-community structure have been based (e.g., by Fleming, 1973; Bourlière, 1989). The Paracou fauna itself may be undersampled for arboreal species, however, which comprise a somewhat smaller proportion of the fauna at this site than at other Neotropical rainforest localities previously analyzed for substrate use (e.g., Kay and Madden, 1997: table 30.4). Based on the list of additional nonvolant species that might yet be recorded in our study area (appendix 1), future inventory work could plausibly bring the numbers of arboreal and terrestrial species in the local community into closer conformance with ratios observed in other Neotropical faunas.

Apparently, the only distinctive community-wide aspect of resource use at Paracou concerns trophic structure. Whereas most species of mammals in both New World and Old World tropical rainforests are said to be primary consumers (feeding primarily on fruits, seeds, nectar, leaves, or other plant tissues; Bourlière, 1973, 1989), species of secondary consumers (faunivores) outnumber primary consumers by a substantial margin at Paracou. Contingency tests suggest that this difference is highly significant for some pairwise comparisons with other well-known Amazonian faunas. At Manu, for example, the numbers of primary and secondary consumers are almost inversely proportional to those observed at Paracou (table 69), and it therefore seems appropriate to consider alternative hypotheses that might account for the preponderance of secondary consumers in our study.

A partial explanation clearly involves sam-

pling artifacts. Primary consumers constitute most of the mammalian biomass in all Neotropical rainforest communities studied to date (Eisenberg and Thorington, 1973; Janson and Emmons, 1990; Peres, 1999), where frugivores and granivores in particular tend to be larger-bodied and/or to maintain higher population densities than most faunivores. In addition, some standard inventory methods are known to produce trophically biased samples of rainforest mammal communities; mistnets, for example, are primarily effective for capturing frugivorous bats (Fleming et al., 1972; LaVal and Fitch, 1977; Kalko et al., 1996; Simmons and Voss, 1998), and conventional traps are most effective for capturing frugivorous-granivorous rodents (Voss and Emmons, 1996; this report). For these reasons, short-term and/or methodologically limited inventories probably tend to overestimate the ratio of primary to secondary consumers in local faunas. Given the inverse correlation between known relative primary consumer diversity and cumulative sampling effort at Paracou (fig. 99), trophic comparisons with less intensively worked sites are obviously problematic.

Indeed, future fieldwork at Manu will probably add more secondary than primary consumers to the species list from that site because 33 out of the 48 additional species that could still be expected there (Voss and Emmons, 1996: appendix 10) are faunivores. However, at least part of the difference in trophic structure between the mammal communities at Manu and Paracou is not artifactual. Many taxa of primary consumers that occur at Manu are widespread in western Amazonia but have no known ecological equivalents at Paracou or in other core-Guianan faunas (e.g., *Caluromysiops, Callithrix, Aotus, Callicebus, Lagothrix, Bassaricyon, Microsciurus,* giant squirrels [*Urosciurus*], *Dinomys, Dactylomys, Sylvilagus*), and several taxa of primary consumers common to both inventories are consistently more speciose at western Amazonian than at Guianan localities (e.g., *Carollia, Platyrrhin-*

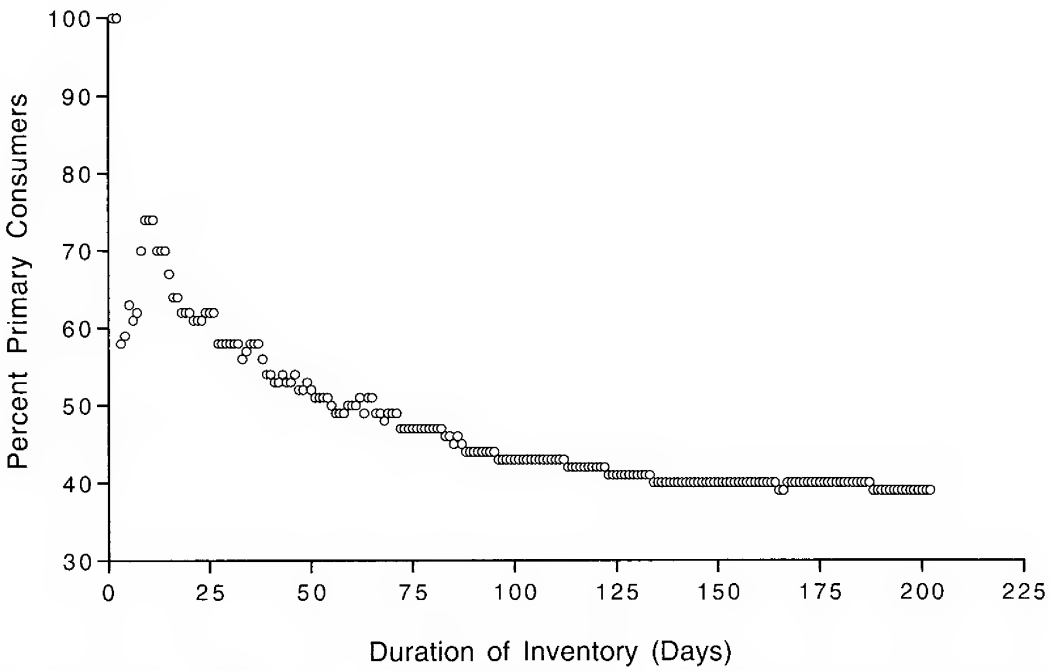

Fig. 99. Percent primary consumers in the known mammal fauna at Paracou (excluding species recorded only from interviews or collections made by previous researchers) on each day of our inventory from 1991 to 1994. From initially high values early in our fieldwork, the proportion of the known fauna represented by primary consumers declined almost monotonically throughout the last half of our fieldwork to a final value of 39%.

us, Uroderma, Saguinus, Proechimys). By contrast, no taxon of primary consumers in the Guianan fauna seems to lack an ecological equivalent in western Amazonia, and no taxon of primary consumers common to both faunas is known to be consistently more speciose at Guianan than at western Amazonian localities. Because secondary consumers appear to be about equally diverse in both Amazonian subregions, at least part of the observed trophic divergence between the Paracou and Manu communities seems to reflect a biogeographic gradient that principally affects the species richness of primary consumers.[32]

SUGGESTIONS FOR FUTURE WORK

Our previous report on the Paracou bat fauna explained the importance for future rainforest mammal diversity research of (1) improving inventory efficiency, (2) establishing standards for reporting inventory data, and (3) using quantitative methods for comparing inventory results from different sites. Although illustrated with chiropteran examples, all of the recommendations made in that report are likewise broadly applicable to nonvolant mammalian surveys. Rather than reiterate such essentially methodological points below, the following topics concern opportunities for advancing the biogeographic synthesis outlined in our general discussion of the Paracou fauna.

Revisionary Taxonomy

The importance of continued revisionary taxonomic research for mammalian biogeographic studies in the rainforested Neotropical lowlands can hardly be overemphasized. Estimates of both local richness and faunal complementarity (endemism) rely crucially on the ability of investigators to distinguish taxa, an ability that is compromised by our currently inadequate knowledge of species limits in many Neotropical clades. Just how much remains to be learned is suggested by the taxonomic results of this study, wherein we applied the most basic of all species criteria (morphological diagnosability) to assign names to voucher material collected at Paracou.

Based on character differences described or referenced in Simmons and Voss (1998) and this report, the following 23 species (newly described or resurrected from synonymy) should be recognized as valid: *Marmosa quichua, Marmosops bishopi, Marmosops juninensis, Marmosops pinheiroi, Monodelphis glirina, Monodelphis palliolata, Centronycteris centralis, Peropteryx trinitatis, Micronycteris brosseti, Micronycteris homezi, Micronycteris microtis, Mimon cozumelae, Eptesicus andinus, Eptesicus chiriquinus, Molossops paranus, Molossus barnesi, Saguinus niger, Neacomys dubosti, Neacomys paracou, Nectomys melanius, Oecomys auyantepui, Coendou melanurus,* and *Mesomys ferrugineus.* Of course, we were not the first to recognize many of these species as valid. Most of the resurrected taxa in this list were originally named as full species and were long recognized as such until synonymized (often with little or no explicit justification) by uncritical advocates of the "polytypic" species concept. More recently, Handley (1976), Brosset and Charles-Dominique (1990), and other cited authors anticipated some of our taxonomic conclusions. However, none of these species were recognized as valid by Wilson and Reeder (1993), whose checklist serves as an adequate summary of the prevailing taxonomic consensus at the time we began our inventory work. By contrast, our results suggest that only two species that Wilson and Reeder recognized as valid should be synonymized: *Choeroniscus intermedius* (with *C. minor*), and *Nectomys parvipes* (with *N. melanius*).

The net change in taxonomic diversity resulting from research with Paracou voucher material, 21 species, represents an increase

[32] Most of the data on which this conclusion is based were summarized by Voss and Emmons (1996), who did not, however, consider their implications for community trophic structure. Our statement about the absence of Guianan primary consumers lacking ecological equivalents in western Amazonia acknowledges the dietary similarity between *Chiropotes* and *Cacajao* (following Ayres, 1989), and our assessment of secondary consumer diversity as approximately equal in Guianan and western Amazonian habitats is based on the fact that several faunivorous bat taxa (e.g., emballonurids, phyllostomines, molossids) have yet to be adequately sampled at any western Amazonian site. Voss and Emmons (1996: table 13) listed *Caluromys* (a marsupial primary consumer) as maximally speciose in the Guianan subregion, but most core-Guianan faunas have only *C. philander.*

of almost 2% over the total Neotropical mammal fauna recognized prior to this study (1145 species according to Patterson, 1994). Because Guianan mammals are relatively well known as a consequence of long accessibility to European naturalists, similarly detailed analyses of voucher material collected in more remote areas (e.g., in western Amazonia; Patton et al., 2000) seem certain to result in substantially larger diversity increments.

Predictably, the improved taxonomic resolution resulting from such research will contribute to a much-needed assessment of biogeographic congruence between mammalian and other biotic distributional data. The close correspondence between spatial patterns of mammalian and avian endemism in the Guiana subregion of Amazonia, for example, is documented herein by numerous distributional data previously obscured by synonymy. Based on our preliminary assessment of many extralimital alpha-taxonomic problems, we anticipate that future research will provide strong mammalian support for many of the endemic patterns first remarked and clearly delimited for Amazonian birds by Cracraft (1985). Many of the molecular results summarized by Patton et al. (1997, 2000) tend to support the same conclusion, in addition to suggesting other patterns of endemism that may exist within recognized avian centers. Plausibly, future revisionary research incorporating both morphological and molecular data will afford the strongest basis for assessing the generality of biogeographic congruence across major clades of Amazonian organisms.

Mapping Guianan Endemicity

Much additional collecting is needed before the geographic range limits of mammals identified herein as Guianan endemics can be mapped with greater confidence. Notably useful would be thoroughly vouchered faunal surveys from northern Brazil, especially (1) in Amazonas and Roraima states between the Rio Negro and the Rio Branco (where most Guianan endemics are apparently absent), (2) in Pará state between the Trombetas and the Jari (an area from which no large faunal lists are apparently available), and (3) from additional sites in Amapá. Special attention should be devoted to the potential existence of a distinctive mammalian fauna in the Amazonian white-water floodplain vis-á-vis the Guianan terra firme in each of these interfluvial zones.

Faunal surveys along the south bank of the Amazon are equally important to test the hypothesis that putative Guianan endemics are not widely distributed there. Indeed, the efficacy of the lower Amazon as a barrier to faunal dispersion should be tested by replicated transects through várzea and terra firme habitats on opposite banks (after Patton et al., 2000). Such transects should devote comparable effort to sampling bat and nonvolant mammalian faunas in order to test the conjecture that riverine barriers are not equally effective for these groups.

Species distributions in the transitional area between the western Amazonian ("Imeri") fauna of southern Venezuela and the Guianan fauna of eastern Venezuela and western Guyana likewise merit targeted fieldwork and careful mapping. Of special interest are the geographic boundaries between such replacing-species pairs as *Philander andersoni/P. opossum, Bradypus variegatus/B. tridactylus, Ateles belzebuth/A. paniscus, Cebus albifrons/C. olivaceus, Dasyprocta fuliginosa/D. leporina,* and *Myoprocta pratti/M. acouchy.* Because most faunal transitions in the Amazonian biota are currently thought to coincide abruptly with very large riverine barriers, the apparently gradual (or stepwise) loss of western Amazonian taxa and their replacement with Guianan forms across hundreds of kilometers of more-or-less continuous Venezuelan lowland forest (Huber and Alarcon, 1982) is of exceptional biogeographic interest.

Historical Connections with Other Areas of Endemism

Phylogenetic analyses of mammalian clades that include endemic Guianan taxa will contribute to an historical assessment of the isolation and assembly of this well-marked center of endemism. Maximally informative analyses with this objective should include morphological and/or molecular terminals from as many areas of Amazonian en-

demism as possible in order to clearly distinguish among alternative biogeographic scenarios. Minimally, taxa inhabiting each of the Napo/Imeri, Inambari, and Rondônia/Pará/Belém centers (after Cracraft, 1985) would appear necessary for any analysis to be informative about the historical biogeography of Guianan endemics.

Unfortunately, the few available phylogenetic datasets that approximate these conditions give contradictory biogeographic indications. The most impressive, Canavez et al.'s (1999) analysis of β_2-microglobulin sequences from *Saguinus* species, suggests that the sister taxon to the endemic Guianan lineage *S. bicolor* + *S. midas* is *S. niger* from southeastern Amazonia (Pará/Belém), a result that implies relatively recent vicariance or dispersal across the lower Amazon. A similar scenario is implied by several of the cytochrome-b sequence analyses reported by Patton et al. (2000: e.g., figs. 171A, 171C), but sister-group relationships between Guianan and western Amazonian haplotypes in other analyses by the same researchers (op. cit.: e.g., figs. 172B, 172D) imply relatively more recent faunal connections across the Rio Negro. Although it is crucial to draw the distinction between haplotypes and taxa in these mitochondrial-gene studies, the prima facie implication of such incongruence is that not all Guianan taxa share the same biogeographic history. Whether any one historical pattern better characterizes the biogeography of Guianan endemics than another will require much more phylogenetic research to convincingly establish.

Causal Explanations for Community Composition

The hypothesis that the mammalian community at Paracou is broadly representative of the Guianan fauna with respect to species richness and trophic structure should be tested with methodologically similar inventory fieldwork at other Guianan sites. Given the essential taxonomic homogeneity of this center of endemism, however, together with the marked tendency for inventory results to converge on geographic expectations with sufficient sampling effort (Voss and Emmons, 1996: fig. 24), it seems probable that such will prove to be the case. If so, then appropriate explanations for these community characteristics should be based on historical and/or ecological circumstances common to the Guianan fauna as a whole rather than on the environmental peculiarities of any particular study site.

Certain paleoenvironmental reconstructions, for example, have suggested that Guianan rainforests were simultaneously isolated and reduced in area during the Pleistocene: by an enormous freshwater lake (e.g., Frailey et al., 1988: fig. 8), or by savannas and other arid vegetation (e.g., Clapperton, 1993: fig. 8). Both scenarios lack convincing independent support (Colinvaux, 1996), but either might explain the lower mammalian species richness of modern Guianan rainforests (as residual insular effects). Neither areal reduction nor isolation, however, plausibly accounts for the conspicuous trophic bias observed in our comparisons of Guianan with western Amazonian mammal communities.

The ancient soils produced by in-situ chemical weathering of the Guiana Shield are routinely characterized as exceptionally nutrient-poor (Jordan, 1985; Sanchez, 1989), especially by comparison with the younger alluvium (mechanically weathered from the Andes) that forms the mineral substrate throughout much of western Amazonia. Poor soils have been hypothesized to negatively affect the species richness of rainforest mammals by constraining plant productivity (Emmons, 1984; Gentry and Emmons, 1987), and it seems intuitively obvious that plant productivity should more directly impact primary consumer than faunivore diversity. Geology therefore offers a superficially plausible explanation for two of the most distinctive contrasts between Guianan and western Amazonian mammal faunas.

The Guianan center of endemism is not, however, coextensive with the Guiana Shield, which extends hundreds of kilometers west of the Rio Negro to the base of the Andes (Gibbs and Barron, 1993), so geology cannot be the whole story. Nor do the climatic maps that we have examined suggest any sharp change in the amount or seasonality of annual rainfall that coincides with the hypothesized limits of the Guianan center of

endemism. Although multifactorial models of plant productivity might reveal some ecologically significant combination of edaphic and climatic variables that broadly characterizes Guianan versus other Amazonian landscapes, it does not seem plausible that ecological gradients alone could result in sharply defined areas of endemism in the absence of historical barriers to dispersal. Given that gradients exist, however, and that taxa differ in their ecological requirements, it would be interesting to explore the possibility (with computer simulations) that semipermeable dispersal barriers might attract species boundaries over many generations in much the same way that they appear to attract step clines in gene frequencies (Endler, 1977). Alternative scenarios for the historical assembly of Amazonian biotas have tended to view major rivers as effective dispersal barriers (e.g., Wallace, 1852; Cracraft, 1985; Ayres and Clutton-Brock, 1992), or as mere hydrological boundaries between ecologically distinctive terrains (Tuomisto and Ruokolainen, 1997). The nature of faunal transitions between mammalian centers of endemism, however, suggests that a more interactive conception of biotic assembly might better fit the facts at hand.

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APPENDIX 1

Nonvolant Mammals Previously Reported from French Guiana or Surinam, but Not Recorded at Paracou

Among the mammals that we did not collect or observe in the course of our fieldwork at Paracou are 23 indigenous nonvolant and nonaquatic species known from other localities in French Guiana or Surinam. Below we cite the original literature for published records and note the existence of voucher material for unpublished range extensions. Habitat associations attributed to species in the following accounts are based on cited published sources, or were inferred from specimen data if no published information was available. French Guianan localities mentioned below are mapped in figure 1.

Our list omits several problematic Surinamese records whose doubtful validity has been discussed elsewhere: *Blarina pyrrhonota* (see Husson, 1978), and *Dasyprocta cristata* and *D. fuliginosa* (see account for *D. leporina,* above). Likewise, we discount as obvious misidentifications Menegaux's (1902) French Guianan records of *Sciurus variabilis* (= *S. granatensis*), *Peromyscus mexicanus, Echimys spinosus* (= *Euryzygomatomys spinosus*), and *Mazama dichotoma* (= *Blastocerus dichotomus*). Honacki et al.'s (1982) description of the range of *Monodelphis americana* as extending to French Guiana and Surinam is also clearly erroneous. Pons and Granjon (1998) listed *Oecomys roberti* and *O. trinitatis* from French Guiana, but we have not personally examined any material unambiguously assignable to those taxa from either French Guiana or Surinam.

Of the 23 species listed below, 12 are unlikely to occur in our study area because they are primarily associated with savannas and other open habitats (*Euphractus sexcinctus, Cerdocyon thous, Odocoileus cariacou, Holochilus sciureus, Sigmodon alstoni, Zygodontomys brevicauda, Cavia aperea, Sylvilagus brasiliensis*), or because they are semiaquatic or littoral species for which suitable riverine habitats are not locally available (*Lontra longicaudis, Pteronura brasiliensis, Procyon cancrivorus, Hydrochoeris hydrochaeris*). Another species (*Neacomys guianae*) probably occurs in rainforest, but its known range does not extend to French Guiana. One rainforest species (*Chiropotes satanas*) is definitely known from French Guiana only in the extreme south of the department, near the Brazilian frontier. The remaining nine species are perhaps widespread in northern French Guiana and might have been locally extirpated in the historic past (*Cebus olivaceus*) or could plausibly be expected to turn up in our study area with additional inventory effort (*Didelphis albiventris, Marmosa lepida, Leopardus tigrinus, Oecomys bicolor, Oecomys rex, Rhipidomys leucodactylus, Echimys chrysurus, Isothrix sinnamariensis*).

1. *Didelphis albiventris*: White-eared opossums were first reported from Surinam by Genoways et al. (1981) and from French Guiana by Julien-Laferrière (1991). Additional French Guianan records were discussed by Catzeflis et al. (1997), who provided compelling documentation that this species inhabits primary lowland rainforest.

2. *Marmosa lepida*: This elusive species has long been known from Surinam (Thomas, 1888; Tate, 1933; Husson, 1978), but the first specimen from French Guiana (MNHN 1998.306) was only recently collected by F. Catzeflis at Les Nouragues. The habitat associations of this species are not well documented, but many of the localities from which it has been reported (especially by Tate [1933] and Morales-Sánchez [1983]) are in densely rainforested landscapes.

3. *Euphractus sexcinctus*: Surinamese records of this rare armadillo were discussed by Husson (1978), but the species has not been reported from French Guiana. Apparently, *E. sexcinctus* is restricted to savannas, open woodlands, and deciduous forests; no vouchered records from rainforest are known (Wetzel, 1982).

4. *Cebus olivaceus*: Apparently, the only published French Guianan records of this rainforest monkey are from Les Nouragues (Julliot and Sabatier, 1993) and Saut Pararé (Guillotin et al., 1994), but the species is probably widely distributed. Three specimens in Paris (MNHN 1962.1344, 1962.1345, 1962.4143) are from "Rivière Marowini", two others (MNHN 1978.321, 1978.322) are from "Crique Elepoussing", and a sixth (AC 1972.176) is from Koulimapopann. Husson (1978) summarized information about Surinamese records.

5. *Chiropotes satanas*: This large and conspicuous rainforest monkey is apparently widespread in Surinam (Husson, 1978; Hershkovitz, 1985), but only two vouchered French Guianan records are accompanied by definite locality data: (1) two specimens (MNHN 1978.326, 1978.327) collected between Trois Sauts and Mont Saint-Marcel, and (2) another pair (AC 1972.173, 1972.174) collected at Koulimapopann; both localities are in or near the Tumuc-Humac mountains near the Brazilian border. The exact provenance of the specimens that Schlegel (1876: 224) reported

from "Oyapock à Cayenne" and from "Oyapock" is unknown.

6. *Cerdocyon thous*: This savanna-dwelling canid (Langguth, 1974) is known from several Surinamese localities (Husson, 1978) but has not been reported from French Guiana.

7. *Leopardus tigrinus*: The original description of this species was based on an 18th-century specimen said to be from Cayenne (Allen, 1919; Husson, 1978), but we are not aware of any recently collected material from French Guiana. A single unvouchered sighting from Les Nouragues (P. Charles-Dominique, personal commun.) appears to be the only known modern French Guianan record, but Husson (1978) described several specimens from Surinam. Oncillas occur in a wide range of habitats, including lowland rainforest (Emmons, 1990, 1997).

8. *Lontra longicaudis*: This rainforest species (Emmons, 1990, 1997) is probably widely distributed in both French Guiana (MNHN specimens are from "Crique Saunier", "Rivière Kaw", "Rivière Oyapock", and Trois Sauts) and Surinam (Husson, 1978). *Lontra longicaudis* has been sighted near Paracou (in a deep tributary stream of the lower Sinnamary River and in mangroves along Crique Malmanoury; P. Petronelli, personal commun.), but never within the 3-km sampling radius around our camp, where streams are probably too shallow and/or intermittent to support otters.

9. *Pteronura brasiliensis*: The type locality of this semiaquatic rainforest species was restricted to French Guiana based on 18th-century observations (see Husson, 1978), but few specimens are apparently known from the department. Two old live-mounts in the MNHN are from "Cayenne" (L. Granjon, personal commun.), and there is a single skin in the same museum from the vicinity of Kaw (MNHN 1990.647, previously misidentified as *Lutra longicaudis*; F. Catzeflis, personal commun.). However, recent sightings have been reported from Les Nouragues, Kaw, Crique Malmanoury, and Crique Angélique (F. Catzeflis and P. Charles-Dominique, personal commun.). Giant otters are still common and widespread in Surinam (Husson, 1978; Duplaix, 1980; Carter and Rosas, 1997).

10. *Procyon cancrivorus*: The crab-eating raccoon was originally described from French Guiana by Cuvier (1798), and two old mounted specimens from "Cayenne" are in the MNHN (L. Granjon, personal commun.). Recent records of French Guianan raccoons are from Petit Saut (Vié, 1999) and Kourou (F. Catzeflis, personal commun.). Husson (1978) summarized Surinamese records of this species. Field observations from the Guianas suggest that *P. cancrivorus* is restricted to mangrove swamps, tidal marshes, and riverbank habitats (Beebe, 1925; Sanderson, 1949; Husson, 1978).

11. *Odocoileus cariacou*: The type locality of the Guianan white-tailed deer (a distinct species from *O. virginianus*; see Molina and Molinari, 1999) was restricted to "Guyane, coastal French Guiana" by Hershkovitz (1948b: 44) and further restricted to Cayenne by Ávila-Pires (1958). There appear to be no other published records of this deer from French Guiana accompanied by definite locality information, but two mounted specimens in the MNHN are from "Guyane" (L. Granjon, personal commun.). Surinamese records were discussed by Husson (1978), who summarized published and unpublished accounts suggesting that Guianan white-tailed deer are primarily associated with savannas and other open habitats.

12. *Holochilus sciureus*: Marsh rats of the genus *Holochilus* were apparently first reported from French Guiana by Charles-Dominique (1993), who identified them as *H. brasiliensis.* Guianan marsh rats, however, more closely resemble *H. sciureus* in the craniodental characters discussed and illustrated by Voss and Carleton (1993). Apparently, the only known French Guianan specimens (in the MNHN) are from the Île de Cayenne. Surinamese collection localities for *Holochilus* were reported by Husson (1978) and Genoways et al. (1981). Like other congeneric species, *H. sciureus* exclusively inhabits open habitats, notably wet grass- and sedge-dominated communities, including marshes, rice fields, wet meadows, and sugarcane plantations (e.g., Twigg, 1962, 1965; Husson, 1978; Genoways et al., 1981).

13. *Neacomys guianae*: Although frequently reported from French Guiana (e.g., by Guillotin, 1982; Charles-Dominique, 1993; Voss and Emmons, 1996: appendix 5), all of the specimens of French Guianan *Neacomys* that we examined represent other species (see the accounts for *N. dubosti* and *N. paracou,* above). Apparently, the range of true *Neacomys guianae* extends from Venezuela eastward through Guyana to Surinam (see table 19, footnote *b*) and does not include French Guiana at all. Although nothing definite has been recorded in the literature concerning the habitats where specimens that we can certainly identify as *N. guianae* were collected, other congeneric species all occur in lowland or lower montane rainforests.

14. *Oecomys bicolor*: French Guianan specimens in the MNHN document the occurrence of this species at Arataye, Cacao, Saül, Trois-Sauts, and "Rivière Approuague". Husson (1978) recorded numerous specimens that he identified as

O. bicolor from Surinam, but Husson's material may have included unrecognized specimens of *O. rutilus.* Most specimens of *O. bicolor* that we examined from French Guiana and elsewhere were collected in rainforested landscapes.

15. *Oecomys rex*: French Guianan specimens in the MNHN document the occurrence of this species on the "Rivière Approuague", and at Arataye, Saül, and Trois Sauts. The species has yet to be reported from Surinam. All specimens of *O. rex* that we have examined were collected in predominantly rainforested landscapes.

16. *Rhipidomys leucodactylus*: The only record of this elusive arboreal species from French Guiana is the holotype of *Rhipidomys leucodactylus aratayae* collected at Saut Pararé on Crique Arataye (Guillotin and Petter, 1984). No records are known from Surinam. Most specimens of *R. leucodactylus* have been collected in rainforested landscapes (Tribe, 1996).

17. *Sigmodon alstoni*: This species has been collected in Surinam (Husson, 1978; Williams et al., 1983; Voss, 1992) and Amapá (Carvalho, 1962), and there is one historical record of a French Guianan specimen from Camopi (Menegaux, 1902). Geographic and ecological data summarized by Voss (1992) indicate that this is a grassland species that does not occur in rainforest.

18. *Zygodontomys brevicauda*: Surinamese and French Guianan records of this species were summarized by Voss (1991), who also documented the exclusively nonforest habitats occupied by mainland forms of *Zygodontomys. Zygodontomys reigi,* named as a new species by Tranier (1976) from French Guianan material, is a junior synonym of *Z. b. microtinus* (see Voss, 1991).

19. *Cavia aperea*: This widespread savanna species (Voss, 1991: 92) is known from Surinam by four specimens collected at a single locality near the Brazilian border (Husson, 1978; Williams et al., 1983). No French Guianan records are known.

20. *Hydrochoeris hydrochaeris*: Capybaras were reported from French Guiana by Charles-Dominique (1993), but only one museum specimen is apparently available from the department (MNHN 1977.540, collected at Trois-Sauts). The closest known sighting to our study area is from the Petit Saut hydroelectric dam site (Vié, 1999). Husson (1978) summarized information about Surinamese specimens and field observations. Although widely distributed in rainforested landscapes, capybaras are semiaquatic and never occur away from rivers, lakes, or marshes (Emmons, 1990, 1997).

21. *Echimys chrysurus*: This arboreal rat has apparently been recorded from only four localities in French Guiana: (1) one specimen (MNHN 1982.1076) collected at Organobo by G. Dubost in 1966, (2) two specimens captured and released in the course of an ecological study at Arataye (Guillotin, 1982), (3) three specimens captured and released in the course of another ecological study at Les Nouragues (F. Catzeflis, personal commun.), and (4) 29 specimens captured and released during faunal rescue operations at Petit Saut (Vié, 1999). Husson (1978) summarized locality information from Surinamese material. Apparently, *E. chrysurus* is only known to occur in rainforest (Emmons, 1990, 1997).

22. *Isothrix sinnamariensis*: This species was recently described from two specimens collected in primary rainforest on the Sinnamary River, about 22 km upstream from the Petit Saut hydroelectric dam site (Vié et al., 1996). Although known from but one locality, this elusive arboreal rat could be expected to occur in lowland rainforest anywhere in French Guiana.

23. *Sylvilagus brasiliensis*: Surinamese records of this rabbit were summarized by Husson (1978) and Hoogmoed (1983); apparently, all are from savannas or open anthropogenic habitats. The species has not been reported from French Guiana.

APPENDIX 2

Species Matrix for 12 Nonvolant Rainforest Mammal Inventories

Below we provide the data on which our quantitative comparisons of nonvolant rainforest mammal faunas are based. The matrix consists of binary presence/absence records (0 = absent, 1 = present) for 176 taxa at 12 Neotropical localities. From left to right, the matrix columns represent La Selva, Barro Colorado, Imataca, Kartabo, Paracou, Arataye, Cunucunuma, MCSE Reserves (Manaus), Xingu, Balta, Manu (Cocha Cashu/Pakitza), and Cuzco Amazónico.

Species records are based on this report and references cited in table 55, but in some cases we scored the presence/absence of higher taxa (e.g., *Neacomys, Nectomys, Mesomys,* and the *parvidens* group of *Marmosa*) due to unresolved issues of voucher identification at one or more inventory sites. Therefore, not all columns in this matrix sum to the same species totals as the corresponding rows of table 55. Note that *Rhipidomys gardneri* Patton et al. (2000) and *Proechimys pattoni*

da Silva (1998) are here used for the species respectively identified as "*Rhipidomys* cf. *couesi*" and "*Proechimys* sp. nov." by Voss and Emmons (1996: appendices 9–11). The squirrel monkeys from Balta reported as *Saimiri sciureus* by Voss and Emmons (1996: appendix 9) are identified below as *S. boliviensis* following Hershkovitz (1984). Other differences in taxonomic usage between Voss and Emmons' (1996) appendices and the following list are explained in the systematic accounts above.

1. *Caluromys derbianus*: 11000 00000 00
2. *Caluromys lanatus*: 00000 01101 11
3. *Caluromys philander*: 00011 11110 00
4. *Caluromysiops irrupta*: 00000 00000 10
5. *Chironectes minimus*: 11011 11001 00
6. *Didelphis albiventris*: 00100 10000 00
7. *Didelphis marsupialis*: 11111 11111 11
8. *Glironia venusta*: 00000 00000 10
9. *Gracilinanus agilis*: 00000 00001 10
10. *Gracilinanus emiliae*: 00001 00000 00
11. *Hyladelphys kalinowskii*: 00001 00000 00
12. *Marmosa lepida*: 00000 10000 00
13. *Marmosa mexicana*: 10000 00000 00
14. *Marmosa murina*: 00111 11111 11
15. *Marmosa robinsoni*: 01000 00000 00
16. *Marmosops noctivagus*: 00000 00001 11
17. *Marmosops "parvidens"*: 00001 10111 11
18. *Metachirus nudicaudatus*: 01111 10111 11
19. *Micoureus demerarae*: 00111 11110 00
20. *Micoureus regina*: 00000 00001 11
21. *Monodelphis adusta*: 00000 00000 01
22. *Monodelphis brevicaudata*: 00111 11110 00
23. *Monodelphis glirina*: 00000 00000 10
24. *Philander andersoni*: 00000 01000 00
25. *Philander mcilhennyi*: 00000 00001 00
26. *Philander opossum*: 11101 10111 11
27. *Bradypus tridactylus*: 00111 10100 00
28. *Bradypus variegatus*: 11000 00011 11
29. *Choloepus didactylus*: 00111 11110 00
30. *Choloepus hoffmanni*: 11000 00001 11
31. *Cabassous centralis*: 11000 00000 00
32. *Cabassous unicinctus*: 00111 00001 00
33. *Dasypus kappleri*: 00111 11101 00
34. *Dasypus novemcinctus*: 11111 11111 11
35. *Priodontes maximus*: 00111 11101 10
36. *Cyclopes didactylus*: 11011 11101 10
37. *Myrmecophaga tridactyla*: 10111 11101 11
38. *Tamandua mexicana*: 11000 00000 00
39. *Tamandua tetradactyla*: 00111 11111 11
40. *Callimico goeldii*: 00000 00000 10
41. *Callithrix pygmaea*: 00000 00000 10
42. *Saguinus fuscicollis*: 00000 00000 11
43. *Saguinus imperator*: 00000 00001 10
44. *Saguinus midas*: 00011 10100 00
45. *Saguinus niger*: 00000 00010 00
46. *Saguinus oedipus*: 01000 00000 00
47. *Alouatta belzebul*: 00000 00010 00
48. *Alouatta palliata*: 11000 00000 00
49. *Alouatta seniculus*: 00111 11101 11
50. *Aotus infulatus*: 00000 00010 00
51. *Aotus lemurinus*: 11000 00000 00
52. *Aotus nigriceps*: 00000 00001 11
53. *Aotus trivirgatus*: 00000 01000 00
54. *Ateles chamek*: 00000 00001 10
55. *Ateles geoffroyi*: 10000 00000 00
56. *Ateles paniscus*: 00011 10100 00
57. *Callicebus brunneus*: 00000 00000 10
58. *Callicebus cupreus*: 00000 00001 00
59. *Callicebus moloch*: 00000 00010 00
60. *Callicebus torquatus*: 00000 01000 00
61. *Cebus albifrons*: 00000 00001 11
62. *Cebus apella*: 00001 10111 11
63. *Cebus capucinus*: 11000 00000 00
64. *Cebus olivaceus*: 00110 11000 00
65. *Chiropotes satanas*: 00000 01110 00
66. *Lagothrix lagotricha*: 00000 00001 11
67. *Pithecia irrorata*: 00000 00000 10
68. *Pithecia monachus*: 00000 00001 00
69. *Pithecia pithecia*: 00111 11100 00
70. *Saimiri boliviensis*: 00000 00001 11
71. *Saimiri sciureus*: 00011 11010 00
72. *Atelocynus microtis*: 00000 00001 11
73. *Speothos venaticus*: 00111 10101 00
74. *Herpailurus yaguarondi*: 11111 10001 11
75. *Leopardus pardalis*: 11111 11101 11
76. *Leopardus tigrinus*: 00100 10000 00
77. *Leopardus wiedii*: 11111 11001 10
78. *Panthera onca*: 11111 10101 11
79. *Puma concolor*: 11111 10101 11
80. *Conepatus semistriatus*: 10000 00000 00
81. *Eira barbara*: 11111 11101 11
82. *Galictis vittata*: 11011 10001 11
83. *Lontra longicaudis*: 11110 11101 11
84. *Mustela* spp.: 10000 00000 01
85. *Pteronura brasiliensis*: 00110 10001 11
86. *Bassaricyon gabbii*: 11000 00001 10
87. *Bassariscus sumichrasti*: 01000 00000 00
88. *Nasua narica*: 11000 00000 00
89. *Nasua nasua*: 00111 11111 10
90. *Potos flavus*: 11111 11111 11
91. *Procyon cancrivorus*: 01010 00001 10
92. *Procyon lotor*: 10000 00000 00
93. *Tapirus bairdii*: 11000 00000 00
94. *Tapirus terrestris*: 00111 11111 11
95. *Pecari tajacu*: 11111 10111 11
96. *Tayassu pecari*: 11111 11101 11
97. *Mazama americana*: 11111 11111 11
98. *Mazama gouazoubira*: 00011 10100 10
99. *Odocoileus cariacou*: 11000 00000 00
100. *Microsciurus alfari*: 11000 00000 00
101. *Microsciurus flaviventer*: 00000 00000 10
102. *Sciurillus pusillus*: 00011 10000 00
103. *Sciurus aestuans*: 00111 10000 00
104. *Sciurus gilvigularis*: 00000 00110 00
105. *Sciurus granatensis*: 11000 00000 00

106. *Sciurus ignitus*: 00000 00001 11
107. *Sciurus igniventris*: 00000 01000 00
108. *Sciurus spadiceus*: 00000 00001 11
109. *Sciurus variegatoides*: 10000 00000 00
110. *Orthogeomys cherriei*: 10000 00000 00
111. *Heteromys desmarestianus*: 11000 00000 00
112. *Melanomys caliginosus*: 10000 00000 00
113. *Neacomys* spp.: 00111 11111 11
114. *Nectomys* spp.: 00111 11011 11
115. *Neusticomys oyapocki*: 00001 00000 00
116. *Neusticomys peruviensis*: 00000 00001 10
117. *Neusticomys venezuelae*: 00010 00000 00
118. *Nyctomys sumichrasti*: 10000 00000 00
119. *Oecomys auyantepui*: 00111 10100 00
120. *Oecomys bicolor*: 01110 11111 11
121. *Oecomys concolor*: 00000 01000 00
122. *Oecomys paricola*: 00000 00010 00
123. *Oecomys superans*: 00000 00001 11
124. *Oecomys rex*: 00110 10100 00
125. *Oecomys roberti*: 00010 00010 01
126. *Oecomys rutilus*: 00011 10000 00
127. *Oecomys trinitatis*: 01000 00010 00
128. *Oligoryzomys* spp.: 11101 10001 11
129. *Oryzomys bolivaris*: 10000 00000 00
130. *Oryzomys emmonsae*: 00000 00010 00
131. *Oryzomys macconnelli*: 00111 10101 10
132. *Oryzomys megacephalus*: 00111 10110 00
133. *Oryzomys nitidus*: 00000 00001 11
134. *Oryzomys perenensis*: 00000 00001 11
135. *Oryzomys talamancae*: 01000 00000 00
136. *Oryzomys yunganus*: 00001 10001 01
137. *Oxymycterus* spp.: 00000 00010 10
138. *Rhipidomys gardneri*: 00000 00000 11
139. *Rhipidomys leucodactylus*: 00000 11000 00
140. *Rhipidomys nitela*: 00111 10110 00
141. *Sigmodontomys alfari*: 10000 00000 00
142. *Tylomys panamensis*: 01000 00000 00
143. *Tylomys watsoni*: 10000 00000 00
144. *Coendou bicolor*: 00000 00001 11
145. *Coendou melanurus*: 00111 00000 00
146. *Coendou mexicanus*: 10000 00000 00
147. *Coendou prehensilis*: 00101 11110 00
148. *Coendou rothschildi*: 01000 00000 00
149. *Hydrochoeris hydrochaeris*: 01110 10011 10
150. *Dinomys branickii*: 00000 00001 10
151. *Dasyprocta fuliginosa*: 00000 01000 00
152. *Dasyprocta leporina*: 00111 10110 00
153. *Dasyprocta punctata*: 11000 00000 00
154. *Dasyprocta variegata*: 00000 00001 11
155. *Myoprocta acouchy*: 00011 10110 00
156. *Myoprocta pratti*: 00000 01001 11
157. *Cuniculus paca*: 11111 11111 11
158. *Dactylomys* spp.: 00000 00011 10
159. *Diplomys labilis*: 01000 00000 00
160. *Echimys chrysurus*: 00000 10110 00
161. *Hoplomys gymnurus*: 10000 00000 00
162. *Isothrix bistriata*: 00000 00000 01
163. *Isothrix pagurus*: 00000 00100 00
164. *Makalata didelphoides*: 00111 10010 00
165. *Makalata occasius*: 00000 00000 10
166. *Mesomys* spp.: 00001 11111 11
167. *Proechimys brevicauda*: 00000 00001 11
168. *Proechimys cuvieri*: 00011 10110 00
169. *Proechimys goeldii*: 00000 00010 00
170. *Proechimys guyannensis*: 00101 11100 00
171. *Proechimys oris*: 00000 00010 00
172. *Proechimys pattoni*: 00000 00001 10
173. *Proechimys semispinosus*: 11000 00000 00
174. *Proechimys simonsi*: 00000 00001 11
175. *Proechimys steerei*: 00000 00001 11
176. *Sylvilagus brasiliensis*: 11100 00011 11